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Volume 35, No. 12, December 1978

Journal de l'office des recherches sur les pêcheries du Canada

Volume 35, nº 12, décembre 1978

Announcements/Avis

Index

An author–subject index and list of publications issued during 1978 will be supplied in early 1979 and distributed free to all *Journal* recipients, including subscribers. Additional copies will be available through the Scientific Information and Publications Branch.

Index

Un index par sujet et auteur et une liste de toutes les publications parues en 1978 paraîtront au début de 1979 et seront distribués gratuitement à tous ceux qui reçoivent le *Journal*, ainsi qu'aux abonnés. On pourra se procurer des exemplaires supplémentaires à la Direction de l'information et des publications scientifiques.

Ichthyoplankton of the St. Lawrence Estuary: Composition, Distribution, and Abundance[1]

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ABLE, K. W. 1978. Ichthyoplankton of the St. Lawrence estuary: composition, distribution, and abundance. J. Fish. Res. Board Can. 35: 1518–1531.

The composition, distribution, and abundance of ichthyoplankton in the St. Lawrence estuary, including adjacent portions of the Saguenay River and the northwestern Gulf of St. Lawrence, were investigated during June–July 1973, June–October 1974, and May–September 1975. The eggs and larvae of 25 species from 14 families (principally osmerids, gadids, cottids, cyclopterids, and pleuronectids) were represented. The larvae, in every year, were almost exclusively forms with demersal eggs. Larvae were consistently more abundant in the upper estuary during every sampling period due to its use as a major spawning and nursery area for several species. Both eggs and larvae were most abundant in June and July. Probable spawning times, areas, and growth of larvae are discussed for selected species.

Key words: ichthyoplankton, St. Lawrence estuary, distribution, larvae, osmerids, gadids, cottids, cyclopterids, pleuronectids

ABLE, K. W. 1978. Ichthyoplankton of the St. Lawrence estuary: composition, distribution, and abundance. J. Fish. Res. Board Can. 35: 1518–1531.

L'auteur a étudié en juin–juillet 1973, juin–octobre 1974 et mai–septembre 1975 la composition, la distribution et l'abondance de l'ichtyoplancton dans l'estuaire du Saint-Laurent, y compris les portions avoisinantes du Saguenay et le secteur nord-ouest du golfe Saint-Laurent. Les oeufs et les larves de 25 espèces appartenant à 14 familles (principalement osmérides, gadidés, cottidés, cycloptéridés et pleuronectidés) sont représentés. A chaque année, les larves sont le composant presque exclusif, avec des oeufs démersaux. Les larves sont toujours plus abondantes dans le haut-estuaire à chaque période d'échantillonnage, parce que cette région est utilisée comme principal lieu de fraie et d'alevinage par plusieurs espèces. Les oeufs et les larves atteignent un sommet d'abondance et juin et juillet. Nous analysons, pour quelques espèces choisies, les époques probables et les régions de fraie, et la croissance des larves.

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THE ichthyoplankton of the St. Lawrence estuary is virtually unstudied. This has occurred despite the fact that it is one of the major estuaries on the Atlantic coast of North America and that estuaries generally have been shown to be important spawning and nursery areas for many species of fish.

Knowledge of the ichthyoplankton of this estuary is limited to a few observations of the occurrence of larval Atlantic herring, *Clupea harengus harengus*, during 1937 (Tremblay 1942) and redfish, *Sebastes*, during June–July 1955 (Day et al. 1957). Jacquaz et al. (1977) studied the ecology of larval capelin, *Mallotus villosus*, in 1974 and 1975.

This paper describes, for the first time, the patterns of ichthyoplankton composition, distribution, and abundance for species other than capelin in the St. Lawrence estuary and discusses probable spawning areas, times, and growth of larvae for selected species.

Materials and Methods

The majority of fish eggs and larvae reported on here were collected during a study of capelin, *Mallotus villosus*, larval ecology in the St. Lawrence estuary and northwestern Gulf of St. Lawrence during June–October 1974 and 1975 (Jacquaz et al. 1977). A detailed description of the sampling techniques is presented there.

Briefly, the sampling scheme consisted of a series of transects across the estuary between Île aux Coudres and Pointe des Monts as well as one (1974) or two stations (1975) at the mouth of the Saguenay River (Fig. 1). The approximate sampling times and locations can be discerned from Fig. 4 for 1974 and Fig. 2 for 1975. Normally, three step oblique tows were made at each station. Each tow was designed to sample a discrete portion of the water column from 0 to 150 m (0–50, 51–100, 101–150 m) in 1974, and

[1]Contribution to the program of GIROQ (Groupe interuniversitaire de recherches océanographique du Québec).

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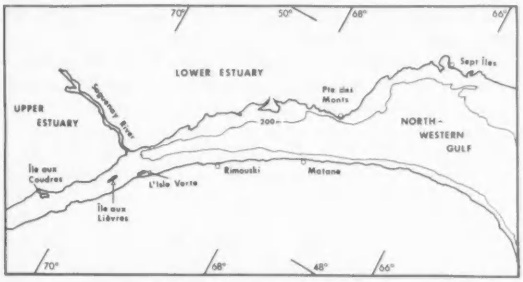


FIG. 1. St. Lawrence estuary and northwestern Gulf of St. Lawrence with important localities mentioned in the text.

0–50, 0–75, and 0–150 m during June, August, and September 1975, respectively. The ranges of actual depths sampled in 1975 are presented in Table 6. The sampling gear consisted of a ½-m Bongo sampler equipped with closing devices and 0.51-mm mesh nets in 1974 and 0.15- and 0.51-mm mesh nets in 1975. To facilitate accurate between year comparisons, the 0.51-mm mesh net sample is used in all determinations of the distribution and abundance of eggs and larvae except where noted.

Additional information was obtained from samples taken by an Isaacs-Kidd midwater trawl (IKMT) fitted with a 1.3-cm liner and a No. 3 (0.32 cm) cod end.

Larvae from collections made in the estuary during June 4–July 13, 1973 were also examined. In this case the sampling gear consisted of a 57-cm plankton net equipped with

TABLE 1. Occurrence of eggs, larvae, egg deposition site, and references that aided in the identification of eggs and larvae for species collected in the St. Lawrence estuary and northwestern Gulf during 1973 (June–July), 1974 (June–October), and 1975 (June–September). E = egg, L = larvae. Eggs were not identified in collections from 1973 and 1974.

Taxa	References	Egg deposition	1973	1974	1975
Clupeidae					
Clupea harengus harengus	Mansueti and Hardy 1967	demersal	L	L	L
Osmeridae					
Mallotus villosus	Templeman 1948	demersal	L	L	L
Osmerus mordax	Templeman 1948	demersal	L	L	L
Gadidae					
Enchelyopus cimbrius	Battle 1929; Faber 1976a	pelagic	L	L	E, L
Gadus morhua	Ryder 1884; Schmidt 1905; Dannevig 1919	pelagic			E, L
Microgadus tomcod	Booth 1968	demersal			L
Urophycis tenuis	Faber 1976a	pelagic	L		
Scorpaenidae					
Sebastes[a]	Templeman and Sandeman 1959	ovoviviparous	L	L	L
Cottidae					
Gymnocanthus tricuspis	Khan 1971	demersal	L	L	L
Myoxocephalus aeneus	Khan 1971; Lund and March 1975	demersal		L	L
M. scorpius	Khan 1971	demersal	L		
Agonidae					
Aspidophoroides monopterygius	Bigelow and Schroeder 1953	demersal	L		L
Cyclopteridae					
Cyclopterus lumpus	Agassiz 1882; Cox 1920	demersal	L		
Liparis atlanticus	Able, unpublished data	demersal	L	L	L
L. cyclostigma	Able, unpublished data	demersal	L	L	L
Anarhichadidae					
Anarhichas[a]	Bigelow and Schroeder 1953	demersal	L	L	L
Lumpenidae					
Leptoclinus maculatus	Faber 1976b	demersal	L	L	L
Lumpenus lampretaeformis	Faber 1976b	demersal	L		L
Stichaeidae					
Ulvaria subbifurcata	Faber 1976b	demersal	L	L	L
Pholididae					
Pholis gunnellus	Bigelow and Schroeder 1953; Ehrenbaum 1905	demersal	L	L	L
Ammodytidae					
Ammodytes[a]	Richards 1965	demersal	L		L
Scombridae					
Scomber scombrus	Sette 1943; Bigelow and Schroeder 1953	pelagic	L		E
Pleuronectidae					
Hippoglossoides platessoides	Petersen 1904; Bigelow and Schroeder 1953	pelagic			E, L
Hippoglossus hippoglossus	Schmidt 1904	pelagic			L
Limanda ferruginea	Perlmutter 1939; Bigelow and Schroeder 1953	pelagic	L		E, L
Totals			20	13	L = 21 E = 5

[a]Identified only to genus because their taxonomy is presently uncertain or the larvae are insufficiently described.

TABLE 2. Abundance (number of individuals/1000 m³) (A), percent frequency of occurrence (B), and number (C) of larvae collected with No. 0 mesh nets in the upper portion of the water column in the St. Lawrence estuary during 1973 (June–July), 1974 (June–September), and in the estuary and northwestern Gulf in 1975 (June–September). Values for rare forms not included.

Taxa	1973			1974			1975		
	A	B	C	A	B	C	A	B	C
Clupea harengus harengus	8.7	24.6	772	43.7	31.3	615	1.9	16.6	107
Mallotus villosus	294.2	74.5	26 259	221.9	52.3	3284	314.6	51.5	16 609
Osmerus mordax	4.5	12.7	404	134.9	17.4	1899	935.0	11.9	50 520
Microgadus tomcod	0	0	0	0	0	0	9.2	7.1	502
Sebastes	0.2	6.7	18	0.5	4.6	8	5.9	13.4	23
Gymnocanthus tricuspis	1.5	7.5	134	1.2	9.3	18	0.1	3.9	7
Liparis atlanticus	0.9	15.7	78	1.1	10.4	16	1.3	19.0	69
L. cyclostigma	9.8	21.6	874	2.4	15.1	34	1.1	16.6	54
Ulvaria subbifurcata	4.3	22.4	385	0.8	8.8	12	0.3	3.9	19
Pholis gunnellus	1.4	34.3	128	0.6	6.9	9	0.2	9.5	12
Ammodytes	8.0	45.5	710	0	0	0	0.2	7.1	9
Limanda ferruginea	6.9	31.3	617	0	0	0	0.3	0.7	2

a 0.51-mm mesh net and a TSK 313 flowmeter. One-half hour tows were taken at 1 and 3 m from the surface. Data from the two depths were combined for the purpose of this study. Sampling locations are indicated in Fig. 6A.

Larval and metamorphosing *Liparis cyclostigma* and larval *L. atlanticus* collected 10–46 and 106–142 cm above the bottom by a plankton net (0.51-mm mesh net) equipped with closing devices (Brunel et al. 1978) were also included in this analysis.

Results and Discussion

SPECIES COMPOSITION

The ichthyoplankton of the estuary is relatively depauperate. During 1973–75 the eggs and larvae of 25 species from 14 families were collected in the estuary and northwestern Gulf (Table 1). Collections in the southern Gulf of the St. Lawrence during essentially the same months have yielded approximately 45 species (Kohler et al. 1976). The most speciose families in the estuary were gadids, cottids, cyclopterids, and pleuronectids (Table 1). The most abundant larvae were those of the osmerids, capelin, *M. villosus* (Jacquaz et al. 1977), and the rainbow smelt, *Osmerus mordax* (Table 2), which together made up 92.1, 87.9, and 98.8% of the total larvae collected during 1973–75, respectively.

SIGNIFICANCE OF DEMERSAL EGGS IN RESIDENT ESTUARINE FISHES

In every year of this study the larvae were dominated by species with demersal eggs (Table 1). In 1973, 1974, and 1975 only 7 of the 25 larval forms collected were from pelagic eggs. An eighth form, *Sebastes*, is ovoviviparous. In 1975, when collections were the most extensive both temporally and spatially, only 27 of the approximately 6×10^5 larvae were from pelagic eggs. Of these only eight were collected in the estuary, the remainder were from the northwestern Gulf. In 1974 all but one and in 1973 98% of the larvae collected were from demersal eggs.

Pelagic eggs did occur in our samples; however, these were usually from nonresident species. In 1975 the eggs of two nonresident species, *Scomber scombrus* and *Gadus morhua*, made up 71.0 and 26.6%, respectively, of all pelagic eggs collected. In 1973, 619 (2%) of the larvae were from pelagic eggs; 617 of these were *Limanda ferruginea*. This species may not spawn regularly in the estuary because it was absent from collection in 1974 and represented by only two larvae in 1975.

Although the sampling occurred only from late May to late October, it seems reasonable to assume that larvae that hatch during other periods in the year would be predominantly from demersal eggs also. Collections made during the winter in other northern estuaries by Chenoweth (1972) and Pearcy and Richards (1962) suggest that the ichthyoplankton at that time would also be composed of forms with demersal eggs such as cottids, stichaeids, and *Pseudopleuronectes americanus*. In addition, other forms that spawn demersal eggs in the estuary were not collected because they have demersal larvae as well. Based on the faunal lists of Vladykov and Tremblay (1935), Vladykov (1961), and our personal observations in the estuary, these would include *Myxine glutinosa*, *Artediellus atlanticus*, *A. uncinatus*, *Eumicrotremus spinosus*, *Careproctus*, two species of *Paraliparis*, and several zoarcids.

Pearcy and Richards (1962) also reported that most resident estuarine fishes in the Mystic River estuary, Connecticut, deposited demersal eggs. They noted that species with demersal eggs (1) were the most abundant in their ichthyoplankton collections, (2) were more common in the upper estuary than the lower estuary, and (3) were most abundant near the bottom. All of these characteristics serve to either decrease drift time, since demersal eggs undergo development while stationary on the bottom instead of drifting with the currents, or increase the possibility of retention in the estuary

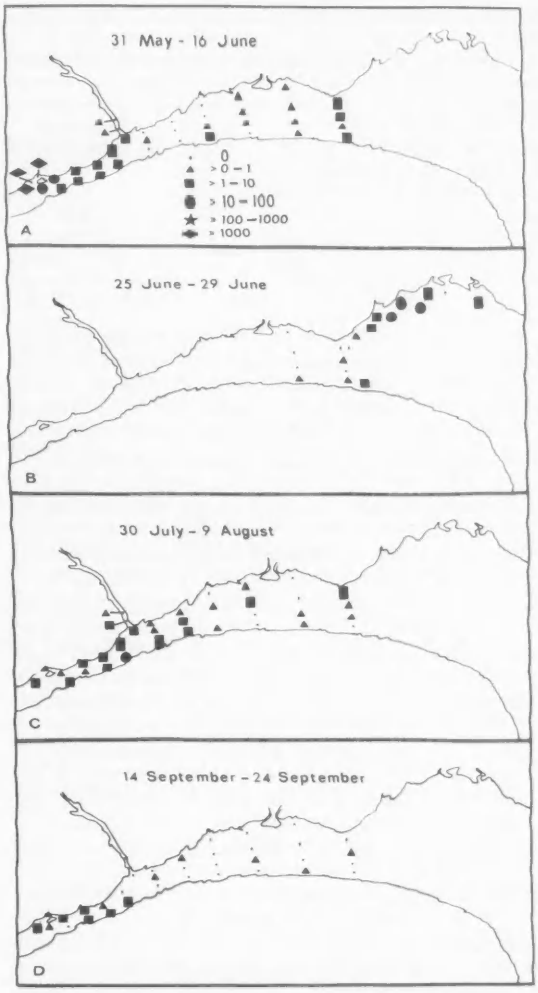


FIG. 2. *Seasonal distribution and abundance of total larvae* in the St. Lawrence estuary and northwestern Gulf of St. Lawrence, 1975, based on Bongo sampler collections.

because upstream countercurrents near the bottom would transport the larvae upstream. The composition of the ichthyoplankton of the St. Lawrence estuary during this study also indicates that the resident estuarine species deposit demersal eggs and suggests that the generalizations of Pearcy and Richards (1962) will be found to apply to the resident fish faunas of most estuaries.

SPATIAL DISTRIBUTION AND ABUNDANCE

During all sampling periods in 1975, the larvae were consistently more abundant in the upper estuary than the lower estuary (Fig. 2). Larval abundance for the upper estuary was 860.3, 3.4, and 1.4 individuals/100 m^3 filtered during the three main sampling periods as compared to 0.4, 1.0, and 0.1 ind./100 m^3 for the same periods in the lower estuary. This distribution was also apparent in Bongo and IKMT samples for the most abundant species, *Clupea harengus harengus* (Fig. 6) and *O. mordax* (Fig. 9), during September–October 1974. This is another pattern also observed by Pearcy and Richards (1962) in their study. The greater abundance of larvae in the upper estuary was due to its use as a major spawning (*M. villosus, C. harengus harengus*) and nursery (*C. harengus harengus, O. mordax*, and *Microgadus tomcod*) area (see Comments on Selected Species).

In direct contrast, the pelagic eggs of *S. scombrus* (Fig. 8), *G. morhua* (Fig. 10), and the larvae of *Hippoglossoides platessoides* (Fig. 5) were virtually absent in the upper estuary, more abundant in the lower estuary, and most abundant in the northwestern Gulf of St. Lawrence.

The vertical distribution of larvae varied with each species; however, most of the abundant species with demersal eggs (*C. harengus harengus, O. mordax, M. tomcod, Liparis atlanticus*, and *L. cyclostigma*) were as or more abundant near the bottom as at the surface. A similar pattern was observed by Pearcy and Richards (1962) in the Mystic River estuary. This again serves to substantiate their comments on the adaptive significance of demersal eggs in resident estuarine fishes.

SEASONAL VARIATION IN ABUNDANCE

In 1975, when sampling was most extensive and intensive, the pelagic eggs and larvae of fishes were most abundant in late May to early June (Table 3). This was especially true of the larvae with 99.4% of all larvae taken in early June. Capelin larval abundance during 1974 and 1975 followed the same pattern (Jacquaz et al. 1977). The decline in abundance of pelagic eggs through the season in 1975 was consistent but not as marked (Table 3).

Comments on Selected Species

ATLANTIC HERRING, *Clupea harengus harengus*

In the estuary herring spawn only in the spring. The larvae appeared first in June and small larvae were still abundant in July but were absent thereafter (Fig. 3). This differs from the southern Gulf of St. Lawrence where both spring and fall spawning occurs (Jean 1956; Day 1957; Leim 1957; Bergeron and Lacroix 1963; Messieh and Kohler 1972). Spring spawning may occur later in the estuary than in the southern Gulf where it is reported as early as late April (Jean 1956). Herring larvae were absent from samples collected in the estuary during May 31–June 16, 1975 (Table 4). A few larvae were collected as early as June 4–9, 1973 and June 7–12, 1974 and were the most abundant and frequent

TABLE 3. Temporal abundance of eggs and larvae in the upper portion of the water column (0–62 m) in the St. Lawrence estuary during 1975.

Sampling period	Sampling depths	Larvae N	Larvae %	Larvae Abundance (no. ind./100 m³)	Eggs N	Eggs %	Eggs Abundance (no. ind./100 m³)
May 31–June 16	0–43	51 087	99.4	248.4	3950	73.3	19.2
July 30–Aug. 9	0–62	242	0.4	1.8	1107	20.5	8.2
Sept. 14–24	0–47	36	0.07	0.4	328	6.0	3.6
Totals		51 362			5385		

form collected during July 2–6, 1974 (Table 4). This suggests that hatching begins in early to mid-June in the estuary. Tremblay (1942) reported similar findings.

Herring larvae were more abundant in the estuary between June 18–July 13, 1973 (Fig. 6A) and July 2–6, 1974 (Table 4) than later in the year. They declined in abundance by September in 1974 and 1975 but were still the most abundant and frequently collected larvae (Table 4) at that time.

The distribution of herring larvae changed seasonally, possibly indicating a movement from spawning to nursery areas. During June and early July of 1973 and 1974 the center of abundance was in the vicinity of Île aux Lièvres and L'Isle Verte in the upper estuary (Fig. 4A) and near Rimouski in the lower estuary (Fig. 4B and 6A). Herring larvae continued to be most abundant near Île aux Lièvres during July 29–August 3, 1974 (Fig. 4C) and July 30–August 9, 1975 (Fig. 5C). At these times they were distributed equally throughout the water column. By late August–September 1974 (Fig. 4D) and 1975 (Fig. 5D) herring larvae were concentrated farther up the estuary than previously, primarily between Île aux Lièvres and Île aux Coudres. This pattern was also evident in IKMT tows made in September (Fig. 6B) and October (Fig. 6C) 1974.

These findings coupled with historical data (Trembly 1942; Day 1957) indicate that the principal area of herring spawning in the estuary is in the vicinity of Île aux Lièvres and L'Isle Verte. Following hatching, the center of larval abundance moves up the estuary and by September is located between Île aux Coudres and Île aux Lièvres. This fall center of abundance approximates the lower limit of the turbidity maximum in the estuary and the area of the steepest temperature and salinity gradients (d'Anglejan and Smith 1973). Concentrations of marine zooplankton in this area are high (Bousfield et al. 1975) and may account for the movement of herring larvae into the area.

Upstream movement of herring larvae may be accomplished by utilizing the residual landward currents which occur near the bottom in the upper estuary (d'Anglejan and Smith 1973; Bousfield et al. 1975; Meric 1975). This movement and the retention of herring larvae may be accomplished by vertical movements of the larvae during the appropriate tidal stages. Graham (1972) has reported a similar pattern of behavior for larval herring in the Sheepscott estuary, Maine.

The growth rate of herring larvae in the St. Lawrence estuary during 1974 and 1975 was similar (Fig. 3). The largest larvae collected during the 2 yr were 25.6 and 26.5 mm (standard length) (Table 5) and the average rate of growth during June–October 1974 was 0.15 mm/d and 0.17 mm/d for June–September 1975.

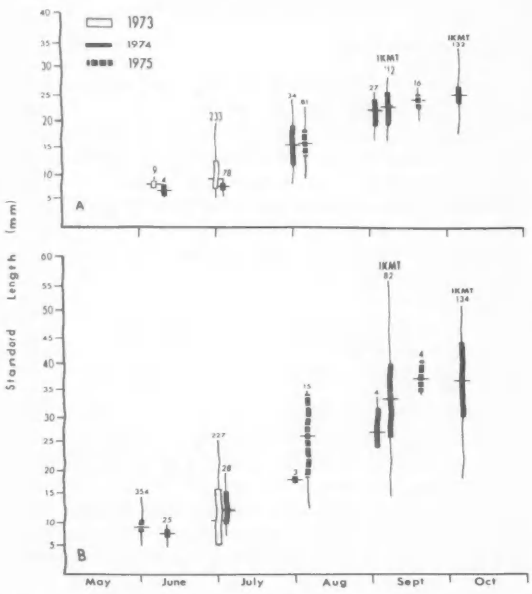


FIG. 3. Growth of larval *Clupea harengus harengus* (A) and *Osmerus mordax* (B) in the St. Lawrence estuary, 1973–75. Narrow vertical line represents the range, the horizontal line, the mean, and the thick vertical line 1 SD on each side of the mean of the standard length.

RAINBOW SMELT, *Osmerus mordax*

The larvae were most abundant in early summer and declined rapidly thereafter. In June 1975 the larvae

TABLE 4. Abundance (number of individuals/1000 m³) (A) and percent frequency of occurrence (B) of larvae collected with No. 0 mesh nets in the upper portion of the water column (range 0–62 m) in the St. Lawrence estuary during 1974 and 1975. Values for rare forms are not included.

	1974								1975					
	June 7–12		July 2–6		July 29–Aug. 3		Aug. 31–Sept. 9		May 31–June 16		July 30–Aug. 9		Sept. 14–24	
Taxa	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Clupea harengus harengus	1.8	6.2	31.7	52.9	13.2	36.0	5.4	28.6	0	0	5.7	38.2	2.0	22.2
Osmerus mordax	12.2	31.2	9.1	35.3	0.7	8.0	0.8	7.1	2455.9	29.7	1.1	5.9	0.4	5.6
Microgadus tomcod	0	0	0	0	0	0	0	0	24.4	24.3	0	0	0	0
Sebastes	0	0	0	0	0.7	8.0	1.0	10.7	0.1	13.5	0.4	17.1	0.3	8.3
Gymnocanthus tricuspis	0	0	0	0	4.3	28.0	0.2	3.6	0.04	2.7	1.2	11.8	0	0
Liparis atlanticus	1.4	18.7	0.3	5.9	2.2	16.0	0.2	3.6	1.3	16.2	3.1	17.6	0.2	2.8
L. cyclostigma	3.2	6.2	1.9	11.7	1.0	12.0	1.6	25.0	0.8	18.9	3.1	32.4	0.2	2.8
Ulvaria subbifurcata	0.4	6.2	2.6	17.6	0.7	12.0	0	0	0.04	2.7	0.2	8.6	0	0
Pholis gunnellus	2.3	31.2	0.3	5.8	0	0	0	0	0.5	21.6	0.1	5.9	0	0
Ammodytes	0	0	0	0	0	0	0	0	0.4	16.2	0	0	0	0

TABLE 5. LENGTH (standard length) of abundant larval forms collected in the St. Lawrence estuary during 1973 (June–July) (No. 0 mesh net), 1974 (June–October) (No. 0 mesh net), and in the estuary and northwestern Gulf during 1975 (June–September) (No. 0 and 10 mesh nets combined).

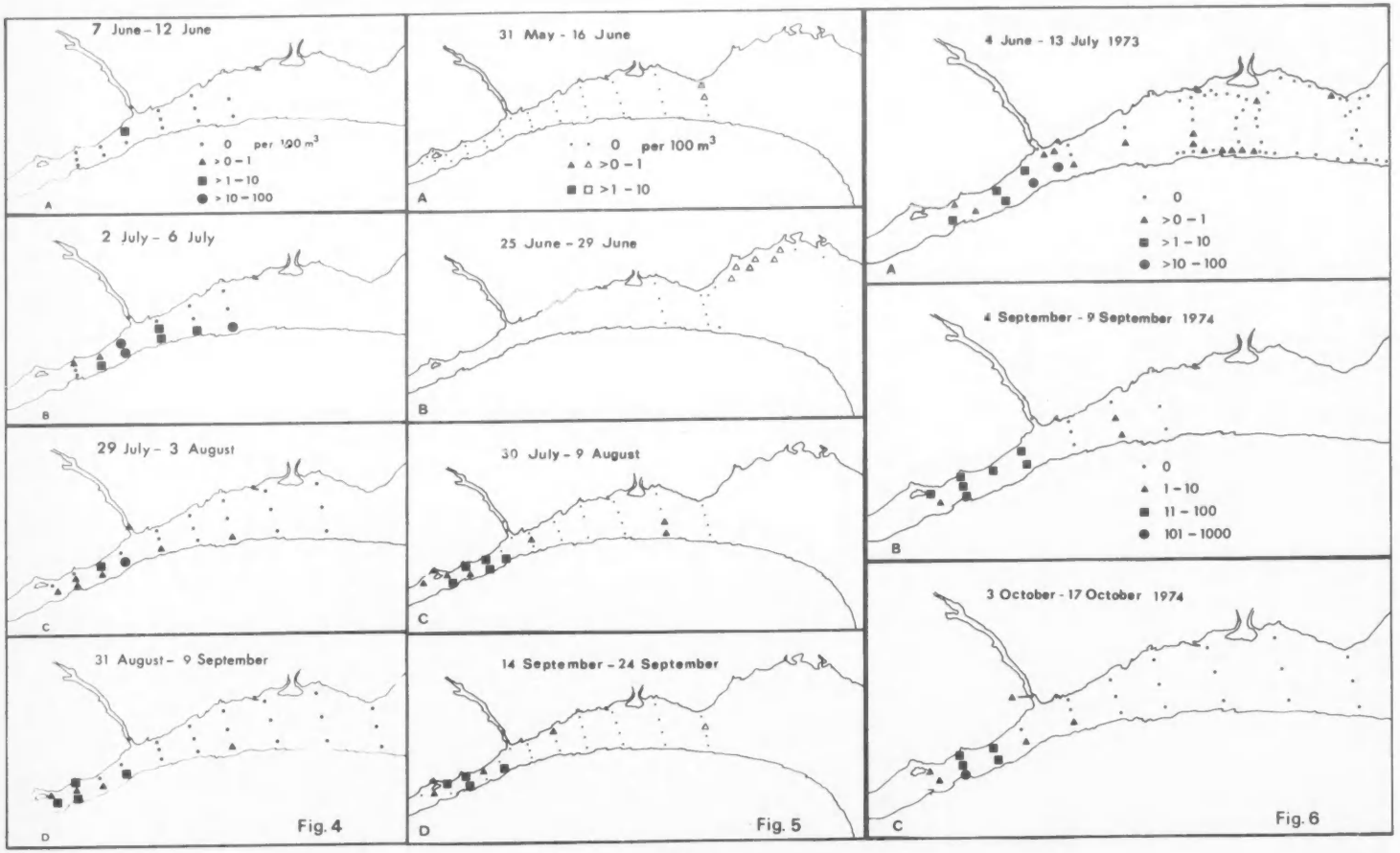
	1973			1974			1975		
Taxa	Range	Mean	*N*	Range	Mean	*N*	Range	Mean	*N*
Clupea harengus harengus	5.0–19.3	9.3	245	5.0–25.6	12.0	393	9.3–26.5	16.6	173
Mallotus villosus				3.7–30.0	7.6	868	3.4–40.2	6.1	2462
Osmerus mordax	5.0–25.3	10.5	207	4.8–33.4	11.6	278	5.1–40.6	9.6	689
Microgadus tomcod	—	—	—	—	—	—	9.3–24.1	15.8	199
Sebastes	6.3–7.6	6.7	18	5.3–8.6	6.2	8	4.2–9.1	6.4	425
Gymnocanthus tricuspis	6.1–9.5	7.5	74	5.6–10.3	7.5	15	5.8–11.2	7.1	26
Liparis atlanticus	3.3–7.3	4.1	67	3.4–5.5	4.7	15	2.7–8.1	4.4	114
L. cyclostigma	4.2–9.0	6.1	216	5.5–15.2	6.6	28	3.3–8.5	5.3	127
Ulvaria subbifurcata	5.2–15.4	6.7	232	5.6–8.6	6.1	12	5.0–7.1	5.8	33
Pholis gunnellus	6.7–27.3	14.7	128	10.1–16.5	13.0	9	10.4–26.1	13.7	27
Ammodytes	4.1–13.8	5.6	432	—	—	—	5.0–25.3	10.2	45
Limanda ferruginea	1.9–5.3	3.2	241	—	—	—	4.9–5.5	—	2

were several orders of magnitude more abundant than in any other month and by July their abundance had decreased dramatically (Table 4). A similar trend was evident in 1974 (Table 4). The decrease in larval smelt abundance was probably due in part to gear avoidance. Smelt larvae were much more abundant in IKMT collections during September 1974 (Fig. 9B) than in the Bongo samplers (Fig. 7D) at the same stations.

Post yolk-sac smelt larvae were abundant in the estuary in early June 1974 and 1975 (Table 4). This suggests the peak of hatching occurred in May and spawning occurred in April–May as recorded by Magnin and Beaulieu (1965). Smelt larvae were one of the most abundant forms collected in the St. Lawrence estuary. They occurred in our collections in every year but were most abundant in the samples from 1975 (Table 2), presumably because of the increased sampling intensity in the vicinity of Île aux Coudres earlier in that year (Fig. 7–9).

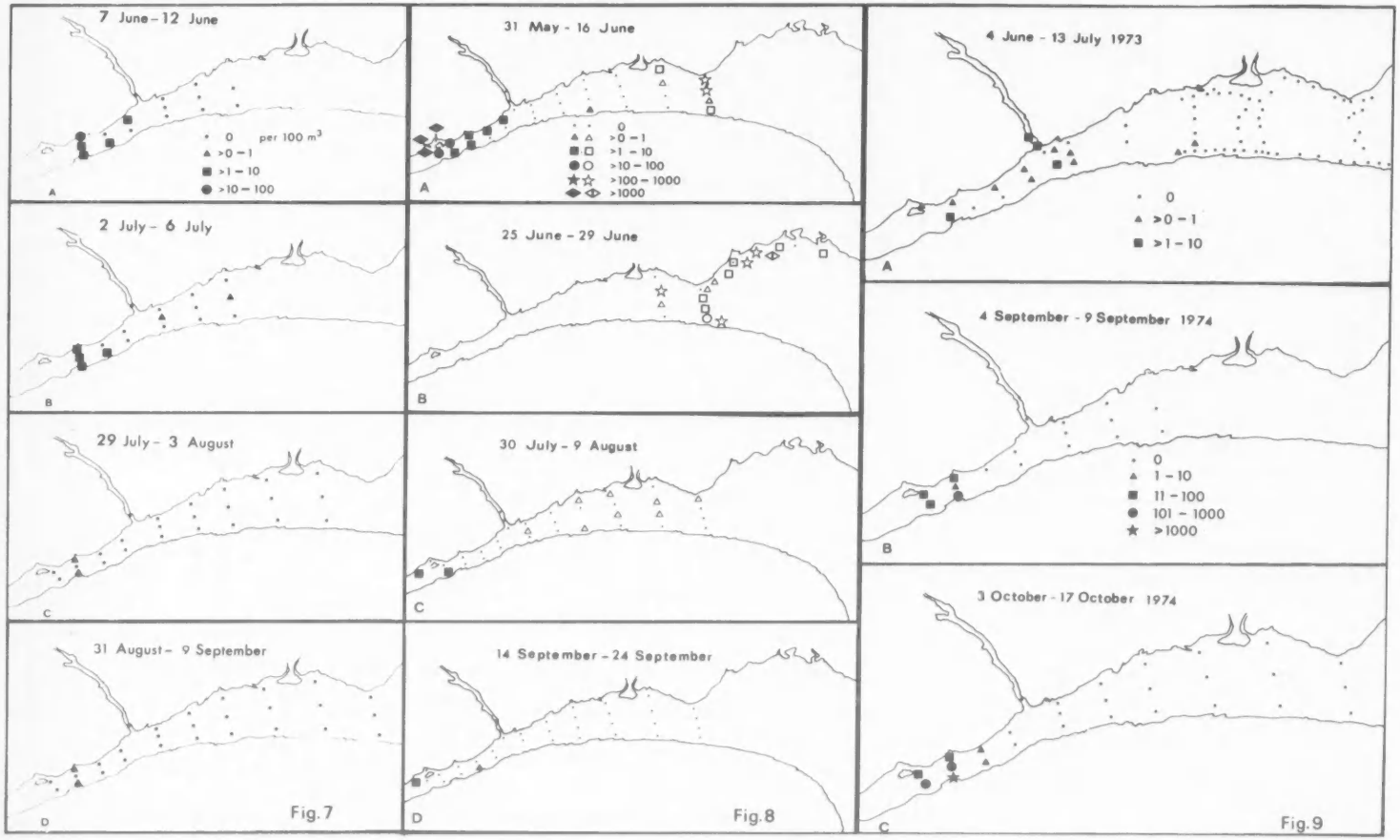
The distribution of smelt larvae in our samples, during all months, is virtually restricted to the upper estuary (Fig. 7–9) and this, despite their abundance, accounts for their low frequency of occurrence (Table 2). In June 1975 smelt larvae were most abundant (maximum 4432 ind./100 m³) around Île aux Coudres (Fig. 8A) and were distributed throughout the water column. Abundance at the surface (1345 ind./100 m³) at this time was slightly less than near the bottom (1662 ind./100 m³). In June and early July 1973, smelt larvae were more abundant in the lower estuary and at the entrance of the Saguenay River (Fig. 9A) than in 1974 (Fig. 7A) when they were never collected in these areas. In September and October 1974, smelt larvae were present in IKMT samples near Île aux Coudres but were more abundant on the south shore of the estuary between Île aux Coudres and Île aux Lièvres (Fig. 9A and B).

The occurrence of smelt larvae in our collections probably covers only a portion of their total distribu-



FIGURES 4–6.

FIG. 4. Seasonal distribution and abundance of *C. harengus harengus* larvae in the St. Lawrence estuary, 1974, based on Bongo sampler collections. FIG. 5. Seasonal distribution and abundance of larval *C. harengus harengus* (solid symbols) and *Hippoglossoides platessoides* (open symbols) larvae in the St. Lawrence estuary and northwestern Gulf of St. Lawrence, 1975, based on Bongo sampler collections. FIG. 6. Seasonal distribution and abundance of *C. harengus harengus* larvae in the St. Lawrence estuary based on 57-cm plankton net collections during 1973 (A) and IKMT collections during 1974 (B and C).



FIGURES 7–9.

FIG. 7. Seasonal distribution and abundance of *O. mordax* larvae in the St. Lawrence estuary, 1974, based on Bongo sampler collections. FIG. 8. Seasonal distribution and abundance of *O. mordax* larvae (closed symbols) and *Scomber scombrus* eggs (open symbols) in the St. Lawrence estuary and northwestern Gulf of St. Lawrence, 1975, based on Bongo sampler collections. FIG. 9. Seasonal distribution and abundance of *O. mordax* larvae in the St. Lawrence estuary based on 57-cm plankton net collections during 1973 (A) and IKMT collections during 1974 (B and C).

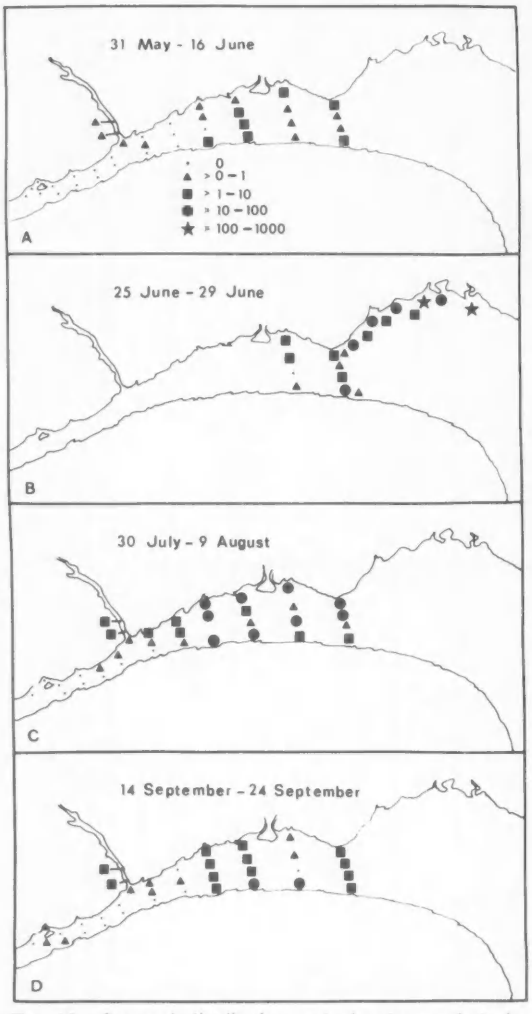


FIG. 10. Seasonal distribution and abundance of *Gadus morhua* eggs in the St. Lawrence estuary and northwestern Gulf of St. Lawrence, 1957, based on Bongo sampler collections.

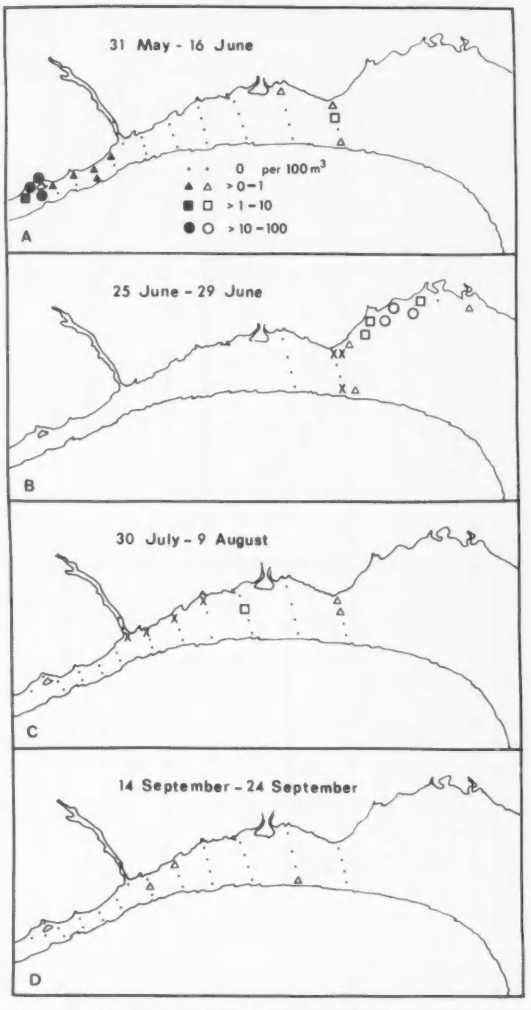


FIG. 11. Seasonal distribution and abundance of *Microgadus tomcod* (closed symbols) and *Sebastes* (open symbols) larvae in the St. Lawrence estuary and northwestern Gulf of St. Lawrence, 1975, based on Bongo sampler collections with a 0.51-mm mesh net. X's indicate station locations where *Sebastes* larvae were absent in the 0.51-mm but present in the 0.15-mm mesh net of the sampler.

tion, since spawning occurs much farther up the estuary (Magnin and Beaulieu 1965) and the larvae were most numerous near the upper limit of our sampling. The lower limit of their occurrence in the estuary, especially in August through October (Fig. 7–9), corresponds with the approximate center of abundance of herring larvae during the same periods (Fig. 4–6).

The collection of smelt larvae in the upper estuary in all months indicates the larvae are capable of maintaining themselves in the upper estuary against the prevailing downstream flow. The greater abundance of smelt near the bottom suggests that they may utilize the upstream currents near the bottom as noted for herring.

The growth of smelt larvae was identical in 1974 and 1975 (0.24 mm/d) and greater than that for herring larvae during this study (Fig. 3). The disparity in larval size between the two species may allow partitioning of the food resource due to differences in prey size selected. This may be especially important in late summer and early fall when they cooccur in the upper estuary.

ATLANTIC COD, *Gadus morhua*

Cod are known to occur as far up the estuary as

TABLE 6. Vertical distribution of Atlantic cod, *Gadus morhua*, and Atlantic mackerel, *Scomber scombrus*, eggs from No. 0 mesh net samples collected in the St. Lawrence estuary and northwestern Gulf (June 25–29) during 1975.

Sampling periods	Sampling depths	*Gadus morhua*			*Scomber scombrus*		
		N	%	Abundance (no. ind./100 m³)	*N*	%	Abundance (no. ind./100 m³)
May 31–June 16	0–4	11	8.0	0.1	3 474	91.1	46.9
	5–20	49	35.7	0.6	327	8.5	4.3
	21–43	77	56.2	1.3	10	0.2	0.1
June 25–29	0–5	999	43.0	29.2	11 636	90.2	340.4
	7–26	940	40.5	24.5	940	7.2	24.5
	24–62	380	16.3	10.1	310	2.4	8.2
July 30–Aug. 9	0–32	525	48.2	7.2	8	100	0.04
	24–62	481	44.1	7.6	—	—	—
	50–111	83	7.6	2.4	—	—	—
Sept. 14–24	0–47	287	87.5	3.1	—	—	—
	45–88	25	7.6	0.4	—	—	—
	75–124	16	4.8	0.3	—	—	—

Kamouraska and Charlevoix counties (Leim and Scott 1966) and Marcotte (1967) has reported on tagging studies at Rimouski, but there was no previous indication that spawning occurred in the estuary.

Spawning in the estuary occurred by early June 1975 since eggs were present at that time (0.7 eggs/100 m³). The number of eggs increased slightly in the last two transects during late June (Fig. 10B) but eggs were most abundant throughout the estuary during late July–early August (6.4 eggs/100 m³) and then declined markedly by September (1.7 eggs/100 m³) (Table 6). Only two cod larvae were collected during this study (July 31 and August 1, 1975).

Cod eggs were most abundant in the lower estuary and northwestern Gulf, although smaller numbers of eggs were collected in the upper estuary and Saguenay River. During early June 1975 the larvae were distributed primarily in the eastern portion of the lower estuary (Fig. 10A). In late June cod eggs were collected at every station in the northwestern Gulf (Fig. 10B). The abundance of cod eggs (21.1 eggs/100 m³) was much greater there than at any time in the estuary. In late July–early August cod eggs were found farther up the estuary (Fig. 10C), and by September a small number of eggs were found at the upper limit of our sampling at Île aux Coudres (Fig. 10D). Cod eggs were collected in the Saguenay River during every sampling period (Fig. 10).

Cod eggs, in contrast to the eggs and larvae of the other species collected in the estuary, were consistently found below ~50 m in the water column (20% of eggs collected July 30–August 9 and September 14–24) (Table 6). This deeper distribution of cod eggs in the estuary could account for their occurrence in the upper estuary and Saguenay River even if spawning did not occur there. Eggs below 50 m in the water column in the lower estuary may be transported up the estuary since net transport below that depth is upstream (Sinclair et al. 1976; Fig. 2). Eggs distributed near the bottom in the upper estuary, as were the eggs collected there during July 30–August 9, 1975 (Fig. 10C), would be transported upstream by the net upstream flow near the bottom (d'Anglejan and Smith 1973; Bousfield et al. 1975; Meric 1975). Similarly, the occurrence of cod eggs in the Saguenay River may be the result of transport there from the surface of the estuary, where they were present, by the local circulation patterns (Therriault and Lacroix 1975).

The pattern of cod egg abundance in 1975 indicates that the size of the spawning population in the estuary in that year was not as great as in the northwestern Gulf and that most of the spawning in the estuary occurred in the eastern portion.

ATLANTIC TOMCOD, *Microgadus tomcod*

Tomcod larvae were collected in our sample only during 1975 (Fig. 11, Table 2) yet they are probably common during most years. This apparent discrepancy in our data is probably due to insufficient sampling around Île aux Coudres during June 1973 and 1974.

Tomcod spawn regularly in the St. Lawrence River from the end of December to January (Vladykov 1955). They occurred in our samples only during June 1975 (Fig. 11, Table 2) and were quite large at that time (Table 5). They may assume a benthic existence at larger sizes since they were absent from Bongo and IKMT samples later in the year, even though large numbers of smelt larvae and juveniles were collected at that time.

The distribution of tomcod larvae in June 1975 (Fig. 11) probably represents only the lower limit of tomcod larval distribution in the estuary. The gradients in temperature and salinity in the vicinity of Île aux Coudres are abrupt, as previously discussed in relation to herring and smelt larvae distribution, and may account for

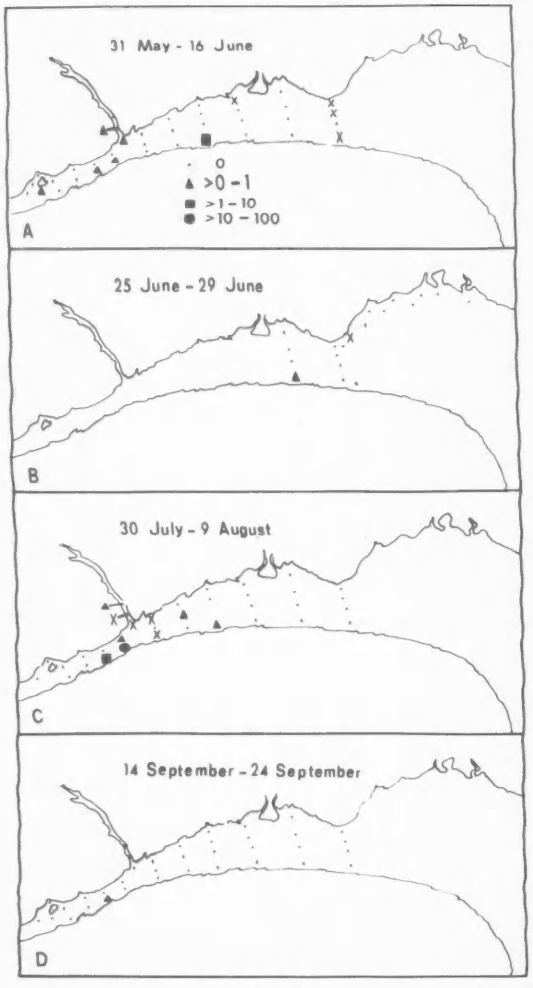


FIG. 12. Seasonal distribution and abundance of *Liparis atlanticus* larvae in the St. Lawrence estuary and northwestern Gulf of St. Lawrence, 1975, based on Bongo sampler collections. X's indicate station locations where larvae were absent in the 0.51-mm but present in the 0.15-mm mesh net of the sampler.

the distribution pattern observed for tomcod larvae also.

During June 1975, 99% of the tomcod larvae in the estuary were collected from the deepest portion of the water column sampled. This pattern was also reported for tomcod larvae in the Mystic River estuary in Connecticut (Pearcy and Richards 1962).

REDFISH, *Sebastes*

Redfish larvae were collected in the estuary during every year of the study, but always in low numbers (Table 2). By contrast, larval abundance was significantly greater in the northwestern Gulf (Fig. 11) than at any time in the estuary. Thus, there do not appear to be large spawning concentrations of redfish in the St. Lawrence estuary. A similar observation, based on trawl survey data, was made by Steele (1957).

SEASNAIL, *Liparis atlanticus* AND DUSKY SEASNAIL, *L. cyclostigma*

Both species spawn as early as June (Table 4). Spawning may continue through the summer since small larvae of each species were collected in September 1975.

The larvae of both species were distributed primarily between Île aux Lièvres and Rimouski in every month in 1975 (Fig. 12, 13). The pattern of vertical distribution for each species was similar as well, with most larvae collected in the deepest portion of the water column sampled or just above the bottom. During late May to early August 1975, 86% of *L. atlanticus* and 79% of the *L. cyclostigma* larvae were found deeper than the surface tow. In addition, plankton samples taken <2 m above the bottom by a plankton net equipped with closing devices collected 21 larval *L. cyclostigma* that ranged from 5.5 to 26.0 mm SL (mean 8.6 mm SL for 12 larvae collected August 13–14, 1973). Similarly 13 *L. atlanticus* larvae taken in the same manner ranged from 3.1 to 5.0 mm SL.

Despite the apparent similarities in timing of spawning, and horizontal and vertical distribution of the larvae of both species, it is possible that they do not compete for food resources since the larvae of *L. cyclostigma* averaged much larger than *L. atlanticus* for all collections in every year (Table 5). Most of this difference is due to the larger size at hatching of *L. cyclostigma* (unpublished data).

SAND LANCE, *Ammodytes*

Sand lance larvae were moderately abundant in the lower estuary below Rimouski during early June 1973 and 1975 (Tables 2 and 4). They were also collected in the northwestern Gulf during June 25–29, 1975. The larvae were concentrated between 0 and 20 m from the surface during 1975. A similar vertical distribution pattern is evident from data for *Ammodytes* in the southwestern Gulf of St. Lawrence (Lacroix and Bergeron 1964).

ATLANTIC MACKEREL, *Scomber scombrus*

Mackerel spawning takes place by mid-June and may extend into August in the estuary. Eggs occurred in samples taken during June 10–16, and through early August 1975 (Table 6).

The major portion of mackerel spawning in the area sampled occurred in the northwestern Gulf in 1975. Although eggs were collected in the last two transects of the estuary during June and a few eggs were col-

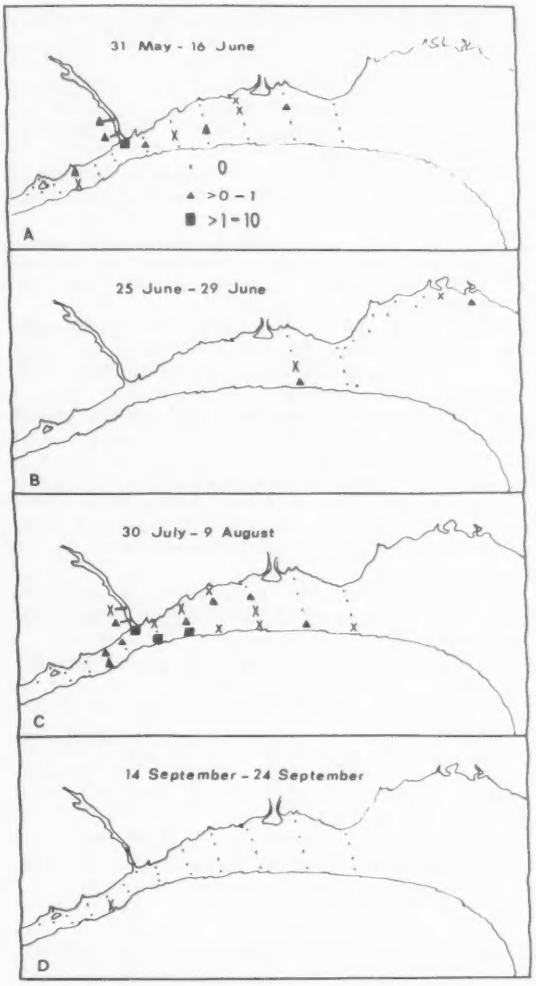


FIG. 13. Seasonal distribution and abundance of *L. cyclostigma* larvae in the St. Lawrence estuary and northwestern Gulf of St. Lawrence, 1975, based on Bongo sampler collections. X's indicate station locations where larvae were absent in the 0.51-mm but present in the 0.15-mm net of the sampler.

lected farther up the estuary in late July and early August, the vast majority of eggs was collected in the northwestern Gulf during late June (Fig. 8). Maximum recorded abundance in the estuary was 226 eggs/100 m^3 while four of eleven stations in the northwestern Gulf exceeded that value, with a maximum abundance there of 1114 eggs/100 m^3.

Most mackerel eggs were collected in surface tows. In the estuary during mid-June, 91.1 and 99.6% of all eggs were collected from 0 to 5 and 0 to 30 m, respectively, from the surface. During late June this pattern was the same with 90.2 and 97.2% found in samples from 0 to 5 and 0 to 26 m, respectively. This pattern of vertical distribution of mackerel eggs has been observed before (Sette 1943).

AMERICAN PLAICE, *Hippoglossoides platessoides*

Plaice eggs and larvae were rare in the estuary and more abundant in the northwestern Gulf in 1975. Plaice eggs were collected during June 10–16, 1975 in the last two transects of the lower estuary and during June 25–29, in the northwestern Gulf. Egg abundance was greater in the latter, especially in the vicinity of Sept Îles. Plaice larvae were collected from the last transect in the estuary during mid-June and mid-September 1975 (Fig. 5A, D) but were more abundant and occurred more frequently in the northwestern Gulf (Fig. 5B) in late June.

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Modification of Phosphorus Retention Models for Use with Lakes with *Low Areal Water Loading*

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OSTROFSKY, M. L. 1978. Modification of phosphorus retention models for use with lakes with low areal water loading. J. Fish. Res. Board Can. 35: 1532–1536.

Existing phosphorus retention models are shown to overestimate retention in lakes where the areal water load (q_s) is <10 m/yr, thereby leading to low predictions of phosphorus concentration. This is caused, in part, by inconsistent assumptions in the overall modeling sequence. New empirical equations are presented that give better predictions of phosphorus for lakes with $q_s < 10$ m, and equally good predictions for lakes with $q_s > 10$ m.

Key words: retention, phosphorus, empirical model, areal water load

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L'auteur démontre que les modèles actuels de rétention du phosphore surestiment cette rétention dans les lacs où la charge par superficie d'eau (q_s) est < 10 m/a, ce qui conduit à de basses prédictions de la teneur en phosphore. Ceci est dû en partie à des hypothèses contradictoires dans la suite ordonnée de la modélisation. On présente de nouvelles équations empiriques donnant de meilleures prédictions du phosphore pour les lacs dont le $q_s < 10$ m et des prédictions également bonnes pour les lacs dont le $q_s > 10$ m.

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RECENTLY, a set of empirical relationships have given limnologists a modeling sequence that may be used to predict the mean concentration of summer chlorophyll-*a* from information contained in geological and topographic maps, aerial photographs, and meteorological summaries (Rigler 1975). One step in this process predicts the phosphorus retention, R_p, of a lake from its areal water load (q_s in metres per year) calculated as Q/A, where Q is the average annual discharge in cubic metres determined from excess precipitation and A is the lake surface area in square metres (Kirchner and Dillon 1975). The relationship not only has given satisfactory predictions of R_p in a variety of areas (Kirchner and Dillon 1975; Scheider 1974; Ostrofsky 1978) but appears to have a sound theoretical basis as well (Chapra 1975).

Nevertheless, there are reasons to suspect the model's predictions for lakes with low values of q_s. In the initial regression analysis between measured R_p and q_s, Kirchner and Dillon (1975) tried several functions (simple exponential, multiple polynomials, etc.) that fit the data equally well but that were all rejected because they gave an intercept of about 0.75. Their rationale was that in a lake with no outflow ($q_s = 0$), all of the entering phosphorus would be retained ($R_p = 1.0$) so logic dictated an intercept of 1.0 regardless of the data. However, they apparently overlooked the implication of a retention of 1.0 for the entire modeling sequence. Since Dillon and Rigler (1974) argued that the phosphorus concentration ($[P_{pred}]$) in micrograms per litre is predicted from the phosphorus loading, J, in milligrams per year, R_p and Q as

$$[P_{pred}] = J(1 - R_p)/Q, \quad (1)$$

they inadvertently suggested that the phosphorus concentration in a lake with no outflow must be 0.0 regardless of the phosphorus loading rate. This is clearly unrealistic. Moreover, the rationale for building empirical models prefers almost by definition to follow empirical relationships rather than argumentation. Both lines of thought suggest that R_p is overestimated.

Moreover, the mathematical relationships between R_p and q_s as suggested by Dillon and Kirchner (1975a) are hyperbolic, and therefore extremely sensitive to small changes in q_s, particularly when q_s is low. Widger and Kimball (1976) were quick to point out that it is not R_p that is of real interest in the modeling sequence, but rather $(1 - R_p)$; thus a seemingly small variation in predicted R_p would give a large error in $(1 - R_p)$. They suggested that the relationship should be used with great care for lakes where q_s was less than ~30 m/yr. This includes 30 of the 42 lakes used to formulate the model.

Because of these problems, errors may be expected in

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the prediction of phosphorus concentration in any lake with low q_s. An opportunity to examine this problem was provided by a unique situation in northwestern Canada. Here there exists an abundance of Shield Lakes in an area that experiences low rainfall (<25 cm/yr) and high evapotranspiration, factors that insure low values for q_s.

Materials and Methods

Fifty-three lakes were selected for examination in the Yellowknife, N.W.T., area (62°25′ – 62°35′N, 113°20′ – 114°42′W) ranging in surface area from 3.8 to 3375 ha, and in areal water load (q_s) from 0.3 to 180 m/yr.

Phosphorus concentration was predicted for each lake using equation (1). The lake surface area (A) and lake catchment area were determined by planimetry from low altitude aerial photographs or 1:50 000 scale topographic maps. The annual discharge of each lake (Q) was then determined as the product of the lake catchment area and the average annual runoff unit ($1.01 \times 10^5\ m^3 \cdot km^{-2} \cdot yr^{-1}$; Morton 1972 unpublished data). Areal water load (q_s) was given by Q/A and the retention of phosphorus, R_p, was estimated using the empirical model provided by Dillon and Kirchner (1975a).

To estimate the loading of phosphorus to the lakes, we considered only aeolian and surface flow inputs. Groundwater was considered unimportant since the low precipitation, shallow overburden, and permafrost layers in the area inhibit the development of extensive subsurface drainage. Cores of undisturbed snow were collected in 12 locations throughout the study area before the onset of the major melting period and were considered to be representative samples of total winter fallout. Six rain collectors were positioned in the study area to collect summer bulk fallout.

To estimate phosphorus export from land surfaces, we sampled 22 streams at weekly intervals from May to September. The total phosphorus load to any lake (J) was the sum of the aeolian contribution to the lake surface and the product of the catchment area and the average phosphorus export. Predicted phosphorus concentrations given by equation (1) will be referred to as $[P_{pred}]$.

Total phosphorus concentrations were measured several times in each lake between ice melt and the onset of permanent thermal stratification, or June 1 for the shallow or exposed lakes that did not stratify. Samples were composites, taken over the maximum depth of the lake with a length of plastic hose with internal diameter of 1.25 cm. The results of these analyses will be referred to as observed phosphorus concentration, $[P_{obs}]$, in micrograms per litre.

All samples collected for phosphorus measurement were analyzed in duplicate using the basic persulfate oxidation technique of Menzel and Corwin (1965) modified somewhat (Seadler and Ostrofsky unpublished data) to eliminate interference from arsenic common in the surface waters of the region.

Results and Discussion

The mean phosphorus concentrations of winter (snow cores) and summer bulk precipitation were 18.7 and 271.8 μg/L, respectively, which indicate an annual aeolian contribution of about 0.4 kg P/ha. This is a similar figure to those found in other studies on the Shield (Schindler and Nighswander 1970; Schindler et al. 1973; Dillon 1974; Ostrofsky 1978), although the total volume of precipitation here was considerably less.

The concentration of phosphorus in each stream was fairly constant throughout the summer. The export then, was taken as the product of the average concentration

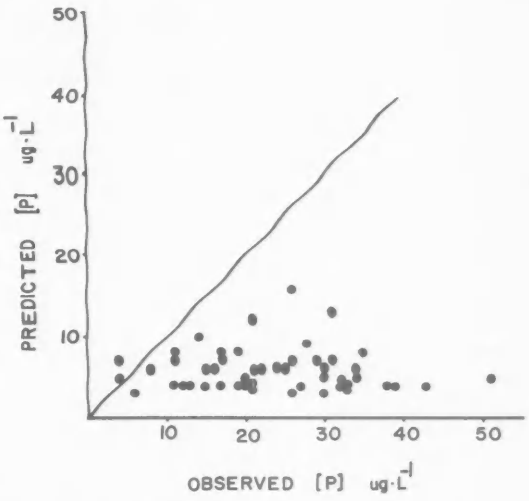

FIG. 1. Relationship between observed spring total phosphorus concentration and phosphorus concentration predicted from equation (1) for 53 lakes. Line is where $[P_{obs}] = [P_{pred}]$.

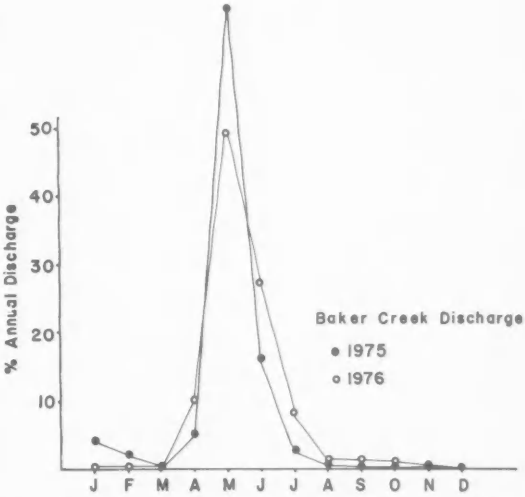

FIG. 2. Hydrograph for Baker Creek, N.W.T. About 80% of the annual discharge occurs during May, June, July, and August.

TABLE 1. Phosphorus budget parameters, and [P_{obs}] for Yellowknife lakes. Annual phosphorus load, J, in kg P/yr; annual lake discharge, Q, in m^3/yr; areal water load, q_s, in m/yr; R_p calculated from Dillon and Kirchner (1975a); [P_{pred}] given by $J(1 - R)/Q$; [P_{obs}] in μg/L.

Lake	J (kg/yr)	Q (m^3/yr)	q_s	R_p	[P_{pred}]	[P_{obs}]	Error ratio
Lake 3	14.7	3.9×10^5	3.1	0.81	7.2	26.4	3.7
Lake 6	81.9	3.0×10^6	20.0	0.40	16.4	26.0	1.6
Lake 5	5.1	7.0×10^4	0.8	0.94	4.1	32.7	8.0
Fiddlers L.S.	76.6	2.3×10^6	5.1	0.72	9.1	28.3	3.1
Fiddlers L.N.	60.6	1.9×10^6	5.7	0.70	9.6	13.5	1.4
Fox	27.7	2.4×10^5	0.4	0.97	3.5	32.3	9.2
Long	65.5	8.9×10^5	0.8	0.94	4.1	16.6	4.0
Stock	27.4	3.2×10^5	0.6	0.95	3.9	33.1	8.5
Frame	44.2	3.7×10^5	0.4	0.97	3.5	20.6	5.9
Grace	91.0	2.7×10^6	4.2	0.76	8.3	35.3	4.3
Lake 1	16.6	3.4×10^5	1.6	0.89	5.2	29.7	5.7
Daigle	14.8	3.9×10^5	3.0	0.81	7.0	16.6	2.4
Finger	2.4	3.9×10^4	1.0	0.93	4.4	11.5	2.6
Shadow	6.2	1.1×10^5	1.3	0.91	4.9	19.8	4.0
X	19.4	6.6×10^5	9.3	0.59	12.1	21.0	1.7
Rater	18.9	4.1×10^5	1.8	0.88	5.5	34.0	6.2
Walsh	515.4	7.2×10^6	0.8	0.94	4.2	14.8	3.5
Vee	57.5	1.2×10^6	1.7	0.88	5.5	30.1	5.5
David	6.6	5.6×10^4	0.4	0.97	3.5	27.1	7.7
Gold	2.9	5.7×10^4	1.5	0.90	5.2	33.5	6.4
Gar	21.6	3.6×10^5	1.1	0.93	4.5	21.0	4.7
Trapper	24.0	5.3×10^5	1.9	0.87	5.7	30.3	5.3
Tibbit L.N.	2 318.8	2.7×10^8	180.8	0.07	8.0	10.5	1.3
Tibbit L.S.	2 354.7	2.7×10^8	133.9	0.09	7.9	11.1	1.4
Lake 50	4.6	3.3×10^4	0.4	0.97	3.4	33.4	9.8
Peninsula	42.5	3.9×10^5	0.5	0.97	3.6	6.4	1.8
Lake 49	18.2	3.6×10^5	2.0	0.87	5.2	15.4	3.0
Lake 48	9.8	2.6×10^5	3.7	0.78	6.9	16.9	2.4
Reid	3 390.0	3.8×10^8	66.6	0.17	7.5	7.9	1.1
Pickerel	95.6	1.5×10^6	0.9	0.94	4.2	18.5	4.4
Lake 47	6.1	3.9×10^4	0.3	0.98	3.3	26.3	8.0
Lake 46	10.4	1.7×10^5	0.8	0.94	4.5	19.8	4.4
Lake 45	54.9	1.2×10^6	2.4	0.85	5.7	21.8	3.9
Lake 44	18.2	6.2×10^5	10.3	0.56	12.5	31.0	2.5
Lake 43	4.1	5.0×10^4	0.7	0.95	3.9	11.1	2.8
Lake 42	2.9	2.2×10^4	0.4	0.97	3.4	30.4	8.9
Lake 41	9.6	1.0×10^5	0.6	0.96	3.7	37.7	10.2
Lake 40	5.6	1.1×10^5	1.4	0.91	5.1	20.9	4.1
Lake 39	28.0	5.7×10^5	1.8	0.88	5.2	21.1	4.1
Lake 38	5.2	7.7×10^4	1.1	0.92	4.2	51.4	12.2
Lake 36	5.6	1.1×10^5	2.2	0.86	5.1	16.4	3.2
Lake 8	43.8	4.6×10^5	0.5	0.96	3.7	43.2	11.7
Pontoon	196.4	2.8×10^6	0.8	0.94	4.1	13.4	3.3
Lake 10 N.	10.6	1.8×10^5	2.5	0.84	4.6	24.8	5.4
Lake 10 S.	7.2	1.8×10^5	1.1	0.92	6.4	19.6	3.1
Madeline	129.2	3.6×10^6	3.7	0.78	7.8	18.7	2.4
Tom	14.9	3.6×10^5	2.4	0.85	6.3	24.2	3.8
Lake 7	34.6	9.2×10^5	3.1	0.81	7.1	29.3	4.1
Fault	3.8	5.5×10^4	0.8	0.94	4.2	39.0	9.3
Shot	15.6	2.6×10^5	1.1	0.92	4.6	31.9	6.9
Little Shot	5.7	1.4×10^5	2.6	0.84	6.5	31.2	4.8
Prosperous	14 856.5	1.6×10^9	47.7	0.22	7.3	4.5	0.6
Prelude	5 334.2	4.8×10^8	14.5	0.48	5.8	3.7	0.6

and the average annual runoff unit. Values ranged from 0.36 to 7.05 kg $P\cdot km^{-2}\cdot yr^{-1}$ (mean 2.57 kg $P\cdot km^{-2}\cdot yr^{-1}$). Again this is similar to published data for other areas of the Shield (Dillon and Kirchner 1975b; Ostrofsky 1978).

Table 1 lists the required data to obtain [P_{pred}] and [P_{obs}] for all lakes. It is apparent that in many cases [P_{pred}] and [P_{obs}] are in poor agreement (Fig. 1). There are at least two possible reasons for the failure of the model to predict [P] more satisfactorily: (1) the ap-

TABLE 2. Examples of retention models that are statistically indistinguishable over the range of the observed data.

$$R_p = 0.6852\, e^{-0.0147 q_s}$$

$$R_p = 0.81 - 2.35 \times 10^{-2} q_s + 3.75 \times 10^{-4} q_s - 2.49 \times 10^{-6} q_s^3 + 5.45 \times 10^{-9} q_s^4$$

$$R_p = 0.75 - 1.40 \times 10^{-2} q_s + 1.08 \times 10^{-4} q_s^2 - 2.66 \times 10^{-7} q_s^3$$

$$R_p = 0.388\, e^{-0.0626 q_s} - 1.790 \times 10^{-3} q_s + 0.400$$

$$R_p = 0.886 - 0.145 \ln q_s$$

$$R_p = 0.201\, e^{-0.0425 q_s} + 0.574\, e^{-0.00949 q_s}$$

$$R_p = \frac{24}{30 + q_s}$$

proach does not apply to this area or (2) there was some error in the estimation of some component(s) of the model, J, Q, and/or R_p. Since the model made satisfactory predictions in other areas, the first alternative is unappealing. There are likely errors in the estimation of Q for 1977 on the basis of long-term average runoff. Further, there may be errors in the estimation of phosphorus loading, J, although the period of sampling covered at least 80% of the annual discharge of streams (Fig. 2). However, the strongest possibility is that the estimation of retention is in error, since very small changes in R_p can have a profound effect on the predictions at low values of q_s.

When the relative error ($[P_{obs}]/[P_{pred}]$) is graphed as a function of q_s for the Yellowknife lakes, and other lakes where reliable phosphorus budget data are available (Fig. 3), the graph suggests first that at q_s values less than ~10 m/yr, there can be large errors in the prediction of phosphorus concentration, and second that $[P_{pred}]$ is always underestimated in this range. Indeed, over the entire range of q_s represented, only in 7 of the 87 lakes is the predicted [P] higher than $[P_{obs}]$. This suggests something other than a random error ($\chi^2 = 61.25$, df = 1) but would result if R_p is overestimated at all values of q_s, particularly at low values.

With the original data of Kirchner and Dillon (1975) and Dillon and Kirchner (1975a) new relationships were sought between q_s and R_p. Again, several functions (simple exponential, multiple polynomial, logarithmic, etc.) fit the data well and an infinite number of plausible solutions could be found giving equally satisfactory results over the range of the observed data. A number of satisfactory solutions are given in Table 2. There were no significant differences between these with respect to either correlation coefficients or residual mean squares, but most important, the intercepts are all <1.0.

None of the models in Table 2 may be defined as a "best fit" equation. Some more than others satisfy our preconception that retention should approach zero as the flow of water through the system, q_s, approaches infinity; however, over the range of the observations (q_s from 0.42 to 223 m/yr, $n = 42$) all are equally adequate for predictive purposes. The double exponential equation was selected from the possibilities on Table 2,

$$(2)\quad R_p = 0.201 \exp(-0.0425 q_s) + 0.574 \exp(-0.00949 q_s)$$

and the data plotted in Fig. 3 were reexamined. Predicted phosphorus concentrations using this modified retention model are much closer to observed concentra-

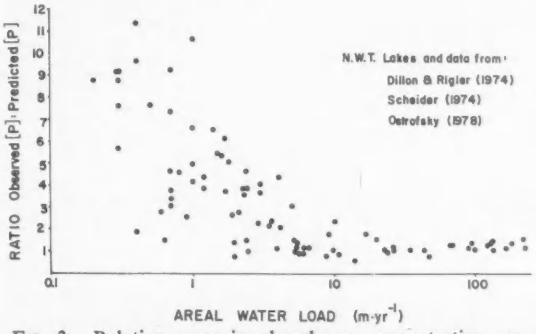

FIG. 3. Relative error in phosphorus concentration prediction ($[P_{obs}]/[P_{pred}]$) as a function of the areal water load (q_s) for 53 N.W.T. lakes and other lakes from the literature.

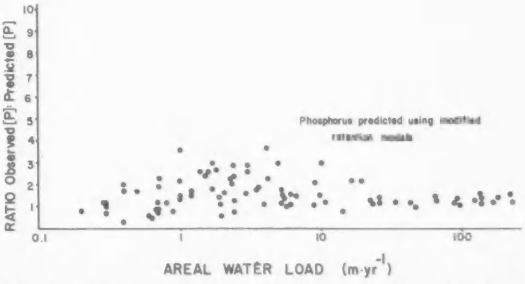

FIG. 4. Relative error in phosphorus concentration prediction as a function of q_s using a revised retention model (equation 2).

tions (Fig. 4). There are still differences between [P_{obs}] and [P_{pred}], probably due to errors in the estimation of J and Q and residual errors in the estimation of R_p. In lakes where q_s is >70 m, the R_p predicted from either model is the same but the revised version (equation 2) permits more realistic predictions where q_s is low.

Undoubtedly, as more data accumulate, further revisions will be necessary and more accurate general predictions will become possible.

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Life History and Taxonomic Status of an Isolated Population of Arctic Char, *Salvelinus alpinus*, from Gros Morne National Park, Newfoundland

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ROMBOUGH, P. J., S. E. BARBOUR, AND J. J. KEREKES. 1978. Life history and taxonomic status of an isolated population of Arctic char, *Salvelinus alpinus*, from Gros Morne National Park, Newfoundland. J. Fish. Res. Board Can. 35: 1537–1541.

Landlocked Arctic char, *Salvelinus alpinus*, from Candlestick Pond, Gros Morne National Park, Newfoundland, were characterized by slow growth, short life span (max 7 yr), and small size (max fork length = 164 mm). Sexual maturity was obtained at age 3, fecundity was low (max 104 ova per fish), and spawning annual. Major food items were zooplankton and aquatic insect larvae. Eight morphometric and eight meristic characters were examined and compared with available literature data for nonanadromous *S. alpinus* in eastern North America. Arctic char from Candlestick Pond were not significantly different from *S. alpinus oquassa* from Quebec and Maine but were significantly different from char from Labrador and other locations in insular Newfoundland. It is proposed that Arctic char from Candlestick Pond are descendents of an aboriginal form of *S. alpinus* that has been largely displaced along the Atlantic coast of North America.

Key words: Salvelinus alpinus, Newfoundland, life history, taxonomic status

ROMBOUGH, P. J., S. E. BARBOUR, AND J. J. KEREKES. 1978. Life history and taxonomic status of an isolated population of Arctic char, *Salvelinus alpinus*, from Gros Morne National Park, Newfoundland. J. Fish. Res. Board Can. 35: 1537–1541.

Les ombles chevaliers, *Salvelinus alpinus*, landlockés de l'étang Candlestick, parc national du Gros Morne, Terre-Neuve, sont caractérisés par une lente croissance, une courte durée de vie (max. 7 ans) et une petite taille (longueur à la fourche max. 167 mm). Ils atteignent la maturité sexuelle à l'âge 3, la fécondité est basse (max. 104 oeufs/poisson) et la fraie est annuelle. Les item alimentaires principaux sont le zooplancton et des larves d'insectes auqatiques. Nous avons examiné huit caractères morphométriques et huit caractères numériques que nous avons comparés avec les données publiées sur *S. alpinus* non anadrome dans l'est de l'Amérique du Nord. Les ombles chevaliers de l'étang Candlestick ne diffèrent pas de façon significative de *S. alpinus oquassa* du Québec et du Maine, mais diffèrent nettement des ombles chevaliers du Labrador et autres endroits de l'île de Terre-Neuve. Nous émettons l'hypothèse que les ombles chevaliers de l'étang Candlestick sont les descendants d'une forme aborigène de *S. alpinus* largement répandue le long de la côte atlantique de l'Amérique du Nord.

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ARCTIC char, *Salvelinus alpinus*, are morphologically variable and the taxonomic status of some forms, including several disjunct, nonanadromous populations in eastern North America, is controversial. The blueback trout, *S. oquassa* (Girard 1854), of Maine, the Sunapee trout, *S. aureolus* (Bean 1887), of Maine and New Hampshire, and the Quebec red trout, *S. marstoni* (Garman 1893), were originally described as separate species. However, the majority of modern opinion supports the hypothesis advanced by Scott and Crossman (1964) and Saunders and McKenzie (1971) that these populations were not distinct from other nonanadromous *S. alpinus* in North America and that specific status was not warranted. Qadri (1974) demonstrated conclusively that the blueback, Sunapee, and Quebec red trouts were conspecific but suggested that they be assigned subspecific status, *S. alpinus oquassa*, because of their geographic isolation.

While these relict populations on the mainland have been examined in some detail, similar nonanadromous Arctic char in insular Newfoundland have received little attention. Scott and Crossman (1964) examined the meristics of a composite sample of 12 fish collected

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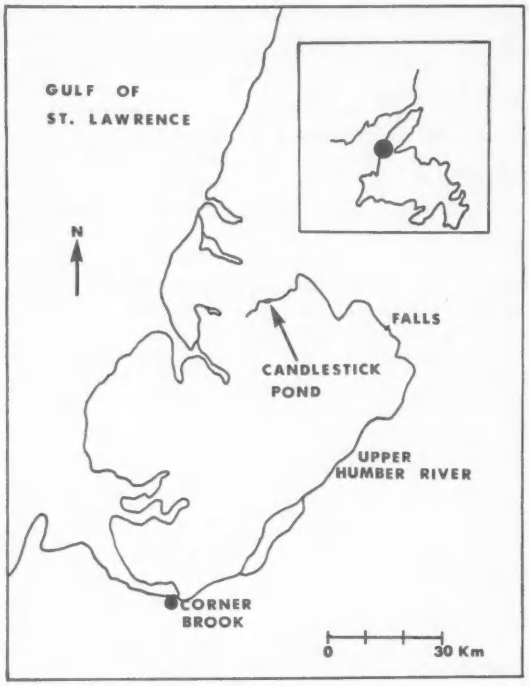

FIG. 1. Location of study area in Gros Morne National Park, Nfld.

from several locations throughout the island and concluded that Newfoundland populations were not distinct from those in either Maine or Labrador. The present study examines in more detail a single landlocked population of Arctic char from Newfoundland and its systematic relationship to other nonanadromous populations of *S. alpinus* in eastern North America.

Study Area

Candlestick Pond (49°58′N, 57°34′45″W) is located in Gros Morne National Park, Newfoundland. It lies in the headwaters of the Upper Humber River at an elevation of 460 m and is effectively landlocked by Main Falls, 45 km downstream (Fig. 1). The pond has a surface area of 0.9 km^2, a mean depth of 4.5 m, and a maximum depth of 16 m. The ice-free period extends from mid-June to late October with a short period of thermal stratification. The pond is highly oligotrophic with a mean salinity of 7.7 mg/L, total phosphorus of 8 mg P/m^3, chlorophyll *a* of 0.3 mg/m^3, pH of 5.1, and an August Secchi disk depth of 4.3 m (unpublished data).

Materials and Methods

On August 19–20, 1976 and June 19–21, 1977 fish collections were made using monofilament gill nets with stretched mesh sizes ranging from 1.3 to 8.8 cm at 1.3-cm intervals. The fork length, weight, sex, and state of maturity of freshly caught fish were recorded. Otoliths (sagitta) were removed and stored dry. The specimens were labeled, fixed in 10% Formalin for 48 h, and stored in 70% ethanol.

The ages of the Arctic char were determined using otoliths and pectoral fin rays. Otoliths were cleaned briefly in 2% HCl and immersed in 50% glycerine at least 2 h before examination. Ages were assigned as described by Grainger (1953). Pectoral fin rays were sectioned near their bases, mounted in glycerine on glass slides, and examined. The criteria used to determine annuli were similar to those of Beamish (1973).

Fecundity counts for mature females collected in August were made and the average diameter of the maturing ova determined.

The stomach contents of fish collected in both August and June were recorded.

Eight morphometric measurements were made on preserved specimens according to the methods of Hubbs and Lagler (1958) and Qadri (1974). These were fork length (FL), head length (H), body length (BdL), distance from the insertion of the dorsal fin to the fork of the tail (pDF), distance between the origins of the pectoral and ventral fins (P–V), distance from the insertion of the dorsal fin to the origin of the adipose fin (D–Ad), distance between the origins of the ventral and anal fins (V–A), and distance from the anterior tip of the lower jaw to the origin of the pectoral fin (Ma–P). Measurements were expressed as a percentage of fork length.

Specimens were lightly stained with Alizarin red to facilitate meristic counts. Eight characters, the number of dorsal, anal, ventral, and pectoral fin rays, the number of gill rakers on the upper and lower limbs of the first gill arch, the number of branchiostegal rays, and the number of pyloric ceca were counted in the manner described by Hubbs and Lagler (1958).

Morphometric and meristic data of the Candlestick Pond Arctic char were compared with available literature values using Student's *t*-test.

Results

Arctic char, ouananiche (*Salmo salar*), and brook trout (*Salvelinus fontinalis*) were captured in Candlestick Pond. The Arctic char made up 27% of the total catch, with 40 taken in August 1976 and 39 in August 1977.

The Arctic char had a dark gray head and back, silver flanks, and a lightly pigmented abdomen. The pectoral, ventral, and anal fins were pale orange with white leading edges. Parr marks were retained by all sexually mature fish and several also displayed subterminal lower jaws and elongate opercula extending past the base of the pectoral fins. Sexual dimorphism was not readily apparent.

The age–length relationships of the char are given in Table 1. The most numerous age-class was 3 yr in August 1976 and the same cohort aged 4 yr in June 1977. Few fish were more than 4 yr old. The oldest Arctic char captured was age 7 with a fork length of 164 mm and a weight of 42 g. There was no significant size difference between sexes.

The weight–length relationship of fish captured in

TABLE 1. Age–length relationship of Arctic char from Candlestick Pond, Nfld. The fork length is given as mean ± SD (number).

Age	August 19–20, 1976 Fork length (mm)	June 19–21, 1977 Fork length (mm)
1	85.8±3.4 (6)	
2	102 (1)	
3	118.6±5.0 (24)	112.4±2.4 (9)
4	132.8±3.4 (4)	121.1±4.4 (22)
5	144±1.4 (2)	132.7±1.2 (3)
6		
7		164 (1)
Total no.	(37)	(38)

TABLE 2. Fork length and the number and size of maturing ova of sexually mature female Arctic char captured in Candlestick Pond, Nfld., August 1976.

Fork length (mm)	Left ovary No. ova	Left ovary Mean diam (mm)	Right ovary No. ova	Right ovary Mean diam (mm)	Total no.
111	28	2.5	52	2.7	80
113	28	3.2	36	2.9	64
118	54	3.2	31	3.2	85
120	21	3.1	45	3.1	64
123	28	2.6	45	2.6	73
124	31	3.1	45	3.1	76
124	51	3.4	16	3.2	67
125	45	3.1	59	3.1	104
126	35	3.1	26	2.8	61
134	51	2.8	47	2.8	98
135	45	3.2	19	3.4	64
143	49	2.8	36	2.8	85
145	35	3.3	55	3.3	90
Mean 126	38.5	3.0	39.4	3.0	78

August was log W = 3.117 log FL − 5.203 while that of June fish was log W = 2.317 log FL − 3.551, indicating a considerable loss of condition over the winter.

There was no significant difference in the number of males and females captured. All fish aged 3 or more years were sexually mature in August indicating that once maturity is reached, spawning occurs every year. There was no significant correlation between fecundity or ovum size and fork length (Table 2). The mean number of ova was 78 ± 14 with a mean diameter of 3.0 mm. A difference was noted in the degree of development of right and left ovaries in most individuals; however, there was no significant trend for the total sample.

Cladoceran zooplankton were observed in 86%, aquatic insect larvae in 14%, and terrestrial insects in 4.5% of the stomachs of those char containing food items in August. Conspicuous species of zooplankton were *Daphnia pulex*, *Erycercus lamellatus*, and *Holopedium gibberum*. Aquatic insect larvae, principally chironomid, stonefly, caddisfly, and mayfly were the only food items observed in fish captured in June.

TABLE 3. Morphometric measurements expressed as a percentage of fork length of Arctic char from Candlestick Pond, Nfld. *A significant difference from values for *S. alpinus oquassa* from Quebec and New England (Qadri 1974).

	N	Ratios (%) Mean ± SD
H/FL	37	23.2±0.97*
BdL/FL	24	84.5±1.40
pDF/FL	24	48.4±1.51
p–V/FL	24	27.8±1.28
V–A/FL	24	19.9±1.38
D–ad/FL	24	21.2±0.96
Ma–P/FL	24	20.1±1.10

TABLE 4. Meristic data of Arctic char from Candlestick Pond, Nfld. *A significant difference from values for nonanadromous Arctic char from both insular Newfoundland (Scott and Crossman 1964) and Labrador (Backus 1957).

	No. of specimens	Mean ± SD (range)
Dorsal rays	37	10.76±0.68 (10–12)
Anal rays	37	9.35±0.75 (8–11)
Pelvic rays	37	8.89±0.37 (8–10)
Pectoral rays	37	12.62±0.59 (12–14)
Gill rakers on upper limb	37	7.41±0.72 (5–8)*
lower limb	37	13.08±0.92 (12–17)*
total arch	37	20.54±1.31 (18–25)*
Branchiostegal rays	37	8.51±0.56 (7–9)
Pyloric ceca	15	32.53±4.29 (25–41)

Morphometric data for Arctic char from Candlestick Pond are summarized in Table 3 and meristic counts in Table 4. All the morphometric data plus the number of branchiostegal rays and gill rakers were compared with the nearest values given by Qadri (1974) for *S. alpinus oquassa* from Maine and Quebec. Only H/FL was significantly different ($P < 0.001$). The numbers of gill rakers and pyloric ceca were compared with values reported by Scott and Crossman (1964) for nonanadromous Arctic char from insular Newfoundland and by Backus (1957) for a nonanadromous population from Labrador. The number of gill rakers, but not pyloric ceca, was significantly different from that of both groups ($P < 0.001$).

Discussion

Arctic char in Candlestick Pond, Nfld., display the slow growth rate (Thomson 1957; Hunter 1970; McCart and Craig 1973), sexual maturity at a small size and an early age (Vladykov 1933; Martin 1955; Backus 1957), and low fecundity (Dunbar and Hildebrand 1952; McCart and Craig 1973) typical of nonanadro-

mous populations of *S. alpinus* inhabiting oligotrophic waters. The growth rate of the Candlestick Pond fish, however, is considerably slower than that of other nonanadromous populations of Arctic char in eastern North America (Scott and Crossman 1964; Everhart and Waters 1965; Saunders and Power 1969) and is more comparable to that occurring at much higher latitudes (McCart and Craig 1973). The slow growth of the Arctic char in Candlestick Pond, despite the relatively southerly location, appears to result from a combination of low pH, low productivity in the pond, and competition for scarce food resources with brook trout and ouananiche.

Qadri (1974) demonstrated that relict populations of Arctic char in Quebec and New England that had originally been described as distinct species (Girard 1854; Bean 1887; Garman 1893) were in fact conspecific. He proposed that they be assigned subspecific status, *S. alpinus oquassa*, on the basis of their geographic isolation from the rest of Arctic char in North America. The present study compared the morphometrics and meristics of these mainland populations with that of Arctic char from Candlestick Pond, Nfld., and indicated that there was no significant difference. It appears that the relict form of Arctic char in eastern North America termed *S. alpinus oquassa* by Qadri (1974) includes at least some Newfoundland populations.

Scott and Crossman (1964) contended that nonanadromous *S. alpinus* in insular Newfoundland were not distinct from nonanadromous populations in Maine or Labrador. The present study, however, indicated that the Newfoundland fish examined by Scott and Crossman (1964) had a significantly different number of gill rakers ($\bar{x} = 22.8$) from Arctic char from Quebec and New England ($\bar{x} = 20.7$–21.4; Qadri 1974), Labrador ($\bar{x} = 24.4$; Backus 1957), and Candlestick Pond ($\bar{x} = 20.5$).

McPhail (1961) demonstrated the importance of the mean number of gill rakers and pyloric ceca in char systematics and indicated that *S. alpinus* from the eastern Canadian Arctic typically had 25–29 gill rakers and 36–53 pyloric ceca. Behnke (1972) noted that certain relict populations of Arctic char in eastern North America had a significantly lower number of gill rakers than other North American Arctic char. These populations appear to be descendents of a form of *S. alpinus*, characterized by a low number of gill rakers, that expanded along the Atlantic coast following the last Pleistocene glaciation. Fish that colonized the postglacial headwaters subsequently became landlocked as a result of isostatic rebound. Behnke (1972) proposed that the aboriginal anadromous form has since been largely displaced or hybridized by the eastern Arctic form described by McPhail (1961) and that its descendents persist only as disjunct, landlocked populations in Newfoundland, Quebec, and New England.

Behnke's (1972) hypothesis provides a plausible explanation for the present distribution of the relict form of *S. alpinus* in eastern North America. The relict populations in Quebec and New England exist well south of the present normal range of Arctic char and it is unlikely that the eastern Arctic form expanded into the region before isolation as a result of isostatic rebound occurred, if at all. The relatively high number of gill rakers of nonanadromous Arctic char from Labrador (Backus 1957), on the other hand, seems to indicate the virtual displacement of the relict form by the eastern Arctic form. The intermediate number of gill rakers reported by Scott and Crossman (1964) for a composite sample of nonanadromous Arctic char from insular Newfoundland may indicate that hybridization between the two forms has occurred. Several of the fish examined by Scott and Crossman (1964) were from locations that were not physically landlocked, which raises the possibility of interbreeding between the aboriginal relict form and the expanding eastern Arctic form. Alternatively, Scott and Crossman (1964) may have inadvertently sampled both relict and eastern Arctic populations and the number of gill rakers that they reported merely reflects a mean value.

Landlocked Arctic char in Candlestick Pond, however, have clearly retained the low number of gill rakers characteristic of the relict form of *S. alpinus*. Insurmountable barriers to fish migration appear to have formed relatively soon after initial colonization as a consequence of the high elevation and long distance from the sea of Candlestick pond and effectively prevented any hybridization with the eastern Arctic form.

Acknowledgments

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Changes in Gill ATPase Activity and Smolt Status of Atlantic Salmon (*Salmo salar*)

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SAUNDERS, R. L., AND E. B. HENDERSON. 1978. Changes in gill ATPase activity and smolt status of Atlantic salmon (*Salmo salar*). J. Fish. Res. Board Can. 35: 1542–1546.

Gill Na^+K^+-activated ATPase activity increased during winter–spring in Atlantic salmon (*Salmo salar*) held at 10°C and subjected to simulated natural or reciprocal (light/dark ratio opposite that of natural) photoperiods. ATPase activity increased earlier and was greater under the reciprocal than under the natural photoperiod regime. Body lipid decreased and moisture content increased sooner and more sharply in reciprocal than in natural photoperiod fish. Salinity tolerance (to 40‰) increased between March and April. Exposure to 40‰ salinity for periods up to 14 d gave marked increases in ATPase activity over levels measured in freshwater. Gill ATPase activity is a sensitive indicator of the ability of Atlantic salmon to osmoregulate in seawater. Together with lipid-moisture content, tolerance to high salinity, and migratory behavior, gill ATPase activity provides a valid indication of smolt readiness to migrate to sea.

Key words: smolt criteria, photoperiod manipulation, Atlantic salmon, smolt physiology, salinity tolerance, osmoregulation

SAUNDERS, R. L., AND E. B. HENDERSON. 1978. Changes in gill ATPase activity and smolt status of Atlantic salmon (*Salmo salar*). J. Fish. Res. Board Can. 35: 1542–1546.

L'activité de l'ATPase activée par Na^+K^+ dans la branchie augmente en hiver et au printemps chez des saumons atlantiques (*Salmo salar*) maintenus à 10°C et soumis à des photopériodes simulées naturelles ou réciproques (rapport clarté/noirceur à l'opposé de la photopériode naturelle). L'activité de l'ATPase augmente plut tôt et davantage sous le régime de la photopériode réciproque que sous celui de la photopériode naturelle. Les lipides corporels diminuent et le contenu en eau augmente plus tôt et de façon plus abrupte avec la photopériode réciproque qu'avec la photopériode naturelle. La tolérance de la salinité (jusqu'à 40‰) augmente entre mars et avril. L'exposition à une salinité de 40‰ durant des périodes allant jusqu'à 14 d produisent des augmentations marquées de l'activité de l'ATPase par rapport aux niveaux observés en eau douce. L'activité de l'ATPase branchiale est un indicateur sensible de l'aptitude osmorégulatrice du saumon atlantique dans l'eau de mer. L'activité de l'ATPase branchiale, couplée à la teneur en lipides et en eau, à la tolérance de fortes salinités et au comportement migratoire, est une indication valide du moment où le smolt est prêt à descendre à la mer.

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A number of physiological, anatomical, and behavioral changes are involved in the parr–smolt transformation which preadapts certain salmonids, while still in freshwater, for life in the sea (Hoar 1976). An important physiological change taking place before diadromous migrations of salmonids is an increase in Na^+K^+-activated ATPase activity in the gill microsomes (Zaugg and McLain 1970; Zaugg and Wagner 1973; McCartney 1976; and Giles and Vanstone 1977). This gill ATPase system is involved in secretion of monovalent ions. The increase in secretory activity begins in salmonids before entry to seawater and may be regarded as one aspect of preadaptation for the transition from freshwater to seawater. In production of salmonids for pen rearing or for release in streams for salmon enhancement projects, it is important to plant smolts at the time when they are prepared physiologically and behaviorally to make the transition from freshwater to the marine environment.

The objectives of this study were to learn whether or not gill ATPase activity changes in response to photoperiod as several other physiological parameters have been shown to do (Saunders and Henderson 1970; Komourdjian et al. 1976) and to assess ATPase activity in comparison with other criteria, such as lipid-moisture content, salinity tolerance, and migratory behavior, used as basis for deciding when to release smolts.

Materials and Methods

In December 1975, two groups of 100 underyearling

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salmon parr were brought to the laboratory and kept at 10°C, one under a simulated natural photoperiod, and the other under a reciprocal photoperiod, i.e. 16 h of light/day beginning in December and decreasing throughout the winter to about 8 h of light/day in June (Komourdjian et al. 1976). Each group was held in a 2-m diam cylindrical fiberglass tank fitted with a submersible pump to create a current. Current velocities near the perimeter were maintained at about 14 cm/s and the fish response was adequate to keep them swimming and prevent resting on the bottom. Thus, activity was similar in both groups. The fish were fed to satiety several times daily with pelleted salmon food.

The method used to determine ATPase activity was that described by Miller et al. (1976) and modified by S. Zell and J. Ray (personal communication) of the University of Maine at Orono. The modifications involved the concentrations of $NaCl_2$, KCl, $MgCl_2$, ouabain, and ATP as well as pH and incubation and reaction times.

Five fish were taken randomly at weekly intervals from each photoperiod group for ATPase, moisture, and lipid measurements. After lengths and weights were measured, the entire gill system of individual fish was removed and the gill filaments trimmed from the arches and placed in an ice-cold solution of 5 mM (5 mmol/L) EDTA and 250 mM (250 mmol/L) sucrose. Gill filaments were blotted on a damp paper tissue and weighed to the nearest 0.01 g. The filaments were ground using a teflon pestle in a glass homogenizer in sufficient EDTA-sucrose to give a 20% homogenate. The homogenizer was packed in a container of crushed ice to keep the sample cold. Three 0.5-mL aliquots of the homogenate were then frozen in 5-mL vials by rotating them in a mixture of dry ice and acetone. Vials were placed on the ports of a freeze-drier and left for 24 h, after which they were stored at −20°C in a freezer until ATPase measurements were made. Preliminary trials indicated that loss of activity occurred if the freeze-dried samples remained in the freezer longer than 2 wk; samples to be used were not stored beyond this period. To reconstitute the freeze-dried homogenate, approximately 5 mL of EDTA-sucrose solution was added to each vial. This brought the protein level of the homogenate to within 0.08–0.11 mg/mL, the optimum level for ATPase measurements. Actual levels of protein were determined by the method of Lowry et al. (1951) using bovine albumin standards and adjustments made if necessary. Na^+K^+-ATPase activity was determined on 0.2 mL of reconstituted gill homogenate from individual fish. After a 5-min incubation period in the assay medium, Na^+K^+-ATPase activity was determined as the difference between the inorganic phosphate liberated from ATP in the presence and absence of 0.2 mM (0.2 mmol/L) ouabain at 37°C. As pointed out by McCarty and Houston (1977), this temperature is nonphysiological for salmonids and ATPase activities measured in this way are uncertain in respect to in vivo conditions. They suggest that assays of gill ATPase activities done at 30°C or higher probably give misleading indications of thermal effects on osmoregulatory capability. However, we believe that valid comparisons can be made between treatment groups in our experiments and with published data obtained in the same way. Final concentrations in the reaction mixtures in mM (mmol/L), were $NaCl_2$, 100; KCl, 20; $MgCl_2$, 5; and ATP, 6 at pH of 7.7. After 10 min, the reaction was stopped by addition of ice-cold color reagent (1% ammonium molybdate in 1.15 N (0.57 mol/L) H_2SO_4) into which 40 mg/mL of ferrous sulfate had been dissolved just before use. After centrifuging, the optical density was measured at 700 nm. Preliminary experiments conducted by Zell and Ray (personal communication) demonstrated that these assay conditions yielded maximal gill Na^+K^+-ATPase activities in salmon gill homogenates. Results are expressed as micromoles of inorganic phosphate per milligram of protein per hour.

Moisture determinations were made on the fish (minus the gills) by drying to constant weight in a forced draft oven at 80°C for 48 h.

Lipid determinations were done on aliquots of the dry ground tissue by column extraction as described by Korn and Macedo (1973) using monofluorotrichloromethane (MF Freon, refrigerant-11).

Results

Gill ATPase activity did not increase during the period January–March in the fish subjected to a simulated natural photoperiod (Fig. 1). Linear regressions, which best describe these data, show a sharp increase in activity in late March–early April with activity continuing at a high level. ATPase activity in response to the reciprocal photoperiod regime was best represented by a semilog regression which shows an early increase in activity during winter–spring in response to the long daylength provided by this light regime at that time (Fig. 1). Although there was an abrupt increase in ATPase activity in the natural photoperiod fish during the middle of the observation period, the activity occurred earlier and was greater in the reciprocal photoperiod fish.

Percentage lipid and moisture content changed in reciprocal fashion during the study (Fig. 2, 3). Linear regressions provided the best representation of these data including lipid levels for natural photoperiod fish in which there was a transient rise in January–February. The rates of decrease in lipid ($P < 0.05$) and increase in moisture ($P < 0.01$) were significantly greater in the reciprocal than in the natural photoperiod fish.

Two salinity tolerance tests were conducted at 40‰

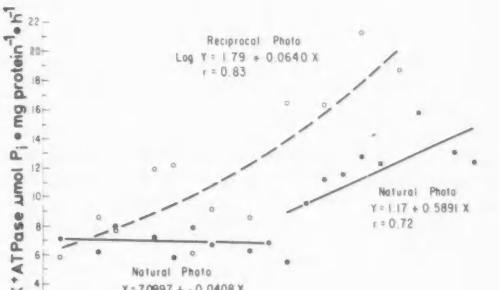

FIG. 1. Seasonal changes in Na^+K^+-activated ATPase levels in response to photoperiod. Each point represents the mean of five determinations.

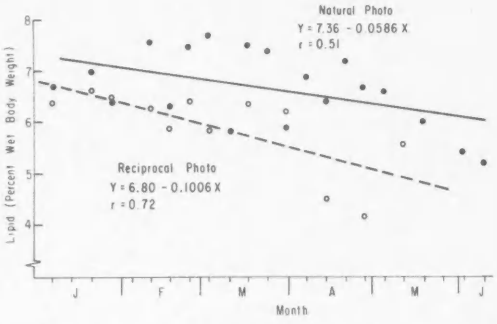

FIG. 2. Changes in total body lipid level in response to photoperiod during winter–spring. Each point represents the mean of five determinations.

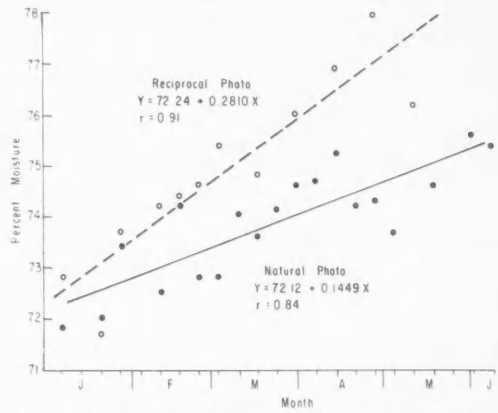

FIG. 3. Changes in moisture content in response to photoperiod during winter–spring. Each point represents the mean of five determinations.

salinity with fish from the natural photoperiod group, one in late March and one in late April. In the first test, 50% of the fish were dead after 50 h. When the fish were challenged with high salinity in April, they displayed a marked tolerance; only one of eight fish had died after 112 h. Following both salinity tolerance tests, the surviving fish were retained in 40‰ for various periods and then sampled for ATPase activity and plasma chloride level. In both cases, ATPase activity increased with length of exposure to high salinity. Plasma chloride level increased during residence in 40‰ salinity and remained about 20 meq/L (mmol/L) higher than for fish in freshwater.

Discussion

Our findings are in agreement with those of McCartney (1976) who reported increased gill Na^+K^+-ATPase activity in Atlantic salmon during spring and peak values corresponding with the usual time of migration to sea. Similar observations have also been made by Zaugg and McLain (1970) and Zaugg and Wagner (1973) for coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Zaugg and Wagner (1973) showed that gill ATPase activity is influenced by photoperiod. ATPase activity, like other smolt criteria studied by Komourdjian et al. (1976), responds to photoperiod manipulation and can be advanced on a temporal basis by subjecting Atlantic salmon to an artificially accelerated spring. The temperature and photoperiod regime in our study was patterned after that used by Komourdjian et al. (1976) in our laboratory. Hence, the results of the two experiments may be compared in respect to other parameters in addition to ATPase activity which was not measured by Komourdjian et al. In agreement with Komourdjian et al., body lipid declined and moisture content increased in reciprocal much earlier than in natural photoperiod fish. The salinity tolerance data in the present experiment are in agreement with those of Komourdjian et al. for natural photoperiod fish. Since the other parameters agree between the two experiments conducted under nearly identical conditions, it is likely that our reciprocal photoperiod fish had increased salinity tolerance in March, as did those of Komourdjian et al., when the natural photoperiod fish had little such tolerance.

Our finding of a dramatic increase in ATPase activity during prolonged residence in seawater was in agreement with those of Zaugg and McLain (1970) and Giles and Vanstone (1976) both working with coho salmon. Not only were the control values for ATPase activity in freshwater higher in late April than in late March, but also the resulting increases in ATPase activity were greater following long exposure to 40‰ salinity. This high ATPase activity together with greater salinity tolerance in late April than was the case a month earlier indicated a greater degree of preadaptation for entry to the sea.

For steelhead trout reared at 6.5 and 10°C, there was a twofold increase in ATPase activity during the spring; at 15°C or higher there was no increase in enzyme activity and little salinity tolerance (Adams et al. 1973). ATPase activity in coho salmon is less temperature sensitive than in steelhead (Zaugg and McLain 1976). Elevated rearing temperatures resulted in increased ATPase activity and accelerated smoltification in coho. Enzyme activity was preserved during long exposure of the fish to 6°C whereas at 10 and 15°C there were decreases following earlier increases. Since our Atlantic salmon developed elevated ATPase levels and salinity tolerance and maintained them while being held during winter–spring at 10°C, it appears that this temperature is not too high for smoltification. Indeed, Komourdjian et al. (1976) found no inhibition of various physiological processes associated with smolting in Atlantic salmon held at 10°C. Elson (1962) reports that seaward movement of naturally produced Atlantic salmon smolts peaks at *ca.* 10°C. Counting fence records from the Northwest Miramichi River, N.B., show few smolts moving downstream after temperatures reach

15°C (R. L. Saunders unpublished data). Possible temperature dependence of ATPase activity in Atlantic salmon at >10°C, like that suggested for Pacific salmonids, should be investigated because hatchery and aquaculture facilities often have such temperatures close to the time that naturally produced smolts are moving to sea.

Our study confirms the findings of Komourdjian et al. (1976) that changes in lipid and moisture content are useful criteria of smoltification. Whereas lipid and moisture contents increase and decrease, respectively, during the summer growth period (Foda 1974), they follow opposite trends during late winter–early spring as smoltification proceeds. Reduced lipid and increased moisture content reflect metabolic changes that accompany smolting and, as such, might be considered as indirect criteria of smolting. However, these changes together with condition factor are clearly associated with smoltification which, judging by other criteria, can be advanced or postponed by manipulating photoperiod as shown by Saunders and Henderson (1970), Komourdjian et al. (1976), and the present study. Farmer et al. (1978) compared the time course of smoltification at two Atlantic salmon hatcheries and found lipid-moisture contents and condition factor to be reliable indicators of the appropriate time to release smolts that developed earlier or later in response to different temperature regimes at the two hatcheries.

A physiological challenge to a salinity as high as 40‰ appears to be an excellent test of sea worthiness but not necessarily of any disposition to move to sea. Wagner (1974b) makes the point that salinity tolerance in salmonids develops many months before smoltification and is separate from smolting. Indeed, salinity tolerance is size dependent (Parry 1958, 1960) and Atlantic salmon of 10–12 cm will live for long periods in seawater of 30‰ salinity (Saunders and Henderson 1969). By challenging juvenile salmonids to 40‰, Komourdjian et al. (1976) and the present study have shown a degree of salinity tolerance that is undeveloped before smoltification and that is an excellent indicator of preparedness for going to sea. Clarke and Blackburn (1977) used seawater challenge as a convenient measure of smolting in Pacific salmon.

Body and fin coloration are useful indications of smolt status in nature. However, most hatchery-reared salmon are more silvery at all stages than wild fish. This is possibly a result of thyroid hormone contained in artificial feeds. Body silvering and particularly fin darkening are pronounced in smolts and are useful indicators of smolt status. Migratory activity as described by Zaugg and Wagner (1973), Wagner (1974a), and Farmer et al. (1978) and observed by many salmon hatchery workers is a useful indicator of readiness of salmon to move downstream when planted in a river.

We conclude that ATPase activity is one of the criteria by which to judge a juvenile Atlantic salmon to be a smolt. Like many of the other parameters studied, ATPase activity in Atlantic salmon responds to photoperiod manipulation. Together with growth pattern, lipid-moisture dynamics, body and fin color, pituitary histology and hormone activity, osmotic–ionic regulation, salinity tolerance, and migratory behavior, ATPase activity serves as an indicator of smolt status and particularly the readiness to begin hyperosmotic regulation.

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The Petroleum-Inducible Mixed-Function Oxidase of Cunner (*Tautogolabrus adspersus* Walbaum 1792): Some Characteristics Relevant to Hydrocarbon Monitoring[1]

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The hepatic aryl hydrocarbon hydroxylase of the cunner (*Tautogolabrus adspersus*) is a sensitive indicator of petroleum contamination. This fish is a particularly favorable species because of its limited home range and ease of capture. Oil concentrations of 1–2 mg/L in water caused two- to sixfold induction of the enzyme above uninduced levels; induction decayed in <7 d after exposure ceased. Feeding of crude oil or mussel tissue contaminated with oil at a concentration of 500 mg/kg caused up to fivefold induction. Males maintained a constant specific activity of aryl hydroxylase through the season, but females had a decreased activity before spawning. Starvation may also have reduced AHH activity. Correlations with liver and body weight were not observed. 2,5-Diphenyloxazole was found to be a safe substitute for benzo[*a*]pyrene in the assay.

Key words: cunner, mixed function oxidase, aryl hydrocarbon hydroxylase, oil pollution, monitoring, biochemistry

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L'aryl hydrocarbure hydroxylase hépatique de la tanche-tautog (*Tautogolabrus adspersus*) est un indicateur sensible de contamination par le pétrole. Ce poisson est une espèce particulièrement commode, à cause de son territoire limité et de la facilité avec laquelle on le capture. Des teneurs en pétrole de 1 à 2 mg/L dans l'eau causent une induction de l'enzyme de deux à six fois supérieure aux niveaux non induits. L'induction disparaît <7 jours après arrêt de l'exposition. L'alimentation au pétrole brut ou au tissu de moule contaminée par le pétrole à une teneur de 500 mg/kg cause une induction pouvant être de cinq fois supérieure. Les mâles maintiennent une activité spécifique constante de l'aryl hydroxylase durant toute la saison, mais les femelles accusent un déclin d'activité avant la fraie. Le jeûne peut également avoir ralenti l'activité de la AHH. Nous n'avons pas observé de relations avec le foie ou le poids corporel. On constate que le 2,5-diphényloxazole peut remplacer le benzo[*a*]pyrène dans l'essai.

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ARYL hydrocarbon hydroxylase (AHH) induction has been proposed by one of us as a sensitive physiological indicator of oil contamination (Payne and Penrose 1975a, b). We demonstrated the induction of benzopyrene hydroxylation in brown trout (*Salmo trutta*) and capelin (*Mallotus villosus*) by exposure to low concentrations of crude oil; also, brown trout from polluted waters had much higher AHH specific activities than those from clean waters. Field observations by Payne (1976) and Stegeman (1978) and a laboratory study by Yarbrough and Chambers (1977) have confirmed the phenomenon. Recently, Kurelec et al. (1977) obtained a series of AHH measurements in *Blennius pavo* before, during, and after an accidental oil spill, which demonstrated a dramatic rise during the period of oil contamination.

The cunner (*Tautogolabrus adspersus*) is a shore-dwelling fish with a very limited home range (Green and Farwell 1971; Green 1975) and occurs from New England to Newfoundland (Leim and Scott 1966). It is easy to capture and maintain, and exhibits a sensitive inducibility of benzopyrene hydroxylase in the presence of petroleum; for these reasons Payne (1976) has suggested its use as a monitoring species. In this work, some important characteristics of the cunner AHH system have been investigated to confirm its suitability as a monitoring tool.

Materials and Methods

Cunners were captured at Portugal Cove and Broad Cove, Newfoundland, with a baited net. They were maintained in flowing seawater on a diet of frozen capelin. Mortality was very low and usualy due to injury.

Mussels (*Mytilus edulis*) were collected from Garden Cove, Newfoundland, and maintained for several months in flowing seawater. Cultures of *Pavlova gyranus* Butcher (Chrysophyceae) were fed to the mussels 2 or 3 times a week; water flow was stopped for about 45 min during feeding to avoid washing out the algae.

In preparation for enzyme assays, fish were killed with a blow to the head. In most experiments, they were sexed, weighed, and measured; the liver was removed and weighed. Gonadal maturity was estimated in some cases. The preparation of liver homogenates and the assay of benzo[*a*]pyrene (BP) hydroxylase have been described previously (Payne and Penrose 1975a). Activity is expressed in terms of arbitrary units of fluorescence at 395 nm excitation and 520 nm emission using a Perkin-Elmer Model 204 fluorescence spectrophotometer. Specific activity was defined in terms of fluorescent units (U) per milligram of protein. Absolute units of activity (usually expressed as pmoles of 3-hydroxybenzopyrene per minute per milligram of protein; Nebert and Gelboin 1968) were not considered necessary because all conclusions were based on relative values. We found 3-hydroxybenzopyrene to be scarce, unstable, and unnecessarily hazardous (like BP, it is also a carcinogen), i.e. unsuitable for routine use as a standard.

2,5-Diphenyloxazole (PPO) was found to be a suitable substrate for the measurement of induction by oil (see also Ahokas 1976). Assays were conducted in the same way as for BP hydroxylase. Each assay contained 10 μg PPO in 20 μL methanol; excitation and emission wavelengths were 345 and 510 nm, respectively. The alkali-solubility of the fluorescent product implies that it is phenolic in character, i.e. a hydroxylation product; we have recently confirmed this supposition by synthesis (W. R. Penrose, L. L. Dawe, R. G. Murphy, and W. P. Gulliver unpublished data).

A Tia Juana Medium crude oil (a gift of Golden Eagle, Ltd.) was used for all experiments. Exposures of fish and mussels to waterborne oil were conducted in flowing seawater. The oil was layered on the surface of the water; water entered the tank above the surface and exited via a siphon that drew water from the bottom of the tank.

Exposures to force-fed or foodborne oil required more complex arrangements to minimize the exposure of gills and other absorptive surfaces to egested or excreted oil. A tank was constructed with individual compartments narrow enough to restrict movements; water entered from a head tank at one end of each compartment and exited through an overflow at the other end. Tests with oil droplets showed the flushing time of the compartments to be only a few seconds. Oil was administered through a pipette directly into the stomach. Tissue from mussels was scraped from the shells, homogenized to a thick paste, and administered through a pipette.

"Accommodated" oil in seawater was measured by the fluorescence method of Keizer and Gordon (1973). A small number of oil particles was found in each sample. Because of the low statistical incidence of, and disproportionately large errors introduced by, these larger particles, there was normally a considerable random error in the measurements. To minimize this error, frequent samples were taken and the data smoothed using moving arithmetic averaging. Methylene chloride used in the oil analyses was made suitable for fluorescence work by distilling from potassium permanganate.

All solvents were spectrophotometric grade, and all other chemicals were reagent grade.

Results

UNINDUCED HYDROXYLASE ACTIVITY

Cunners are normally active at water temperatures above 5°C, and all experiments were done while sea temperatures were between 7 and 13°C. During this period, fish were captured and hepatic BP and PPO hydroxylation measured; length, weight, and liver weight were also measured. In the prespawning samples, the activities in females were about half that of males, but the difference disappeared following the period of spawning in late July (Table 1). The female decline was evident in fish kept 2 yr in a tank at ambient sea temperature but exposed to an uncontrolled lighting regime. Another group of fish kept 1 yr under similar conditions and measured after the usual spawning period showed equal activities between the sexes.

The nutritional history of most animals has a profound effect on liver composition. To examine the effect on hydroxylase specific activities, two groups of cunners were kept for 8 wk during the postspawning period; one group was starved and the other fed ad lib. with capelin. At the end of this time, it was found that both specific

TABLE 1. Sex difference in specific activity of hepatic aryl hydroxylation samples before and after the spawning season. Two samples of fish kept captive for long periods were also included. Specific activities were expressed as the mean ± SD of the number of observations shown in units defined in Materials and Methods. *P* is the probability of the null hypothesis (equal specific activities between the sexes). Substrate is PPO except for the bracketed data, which are for BP.

Date	Source of sample	Specific activity		*P*
		Male	Female	
July 18, 1977	Field, prespawning	20.5±5.38 $n = 8$	5.9±2.79 $n = 10$	<.01
Aug. 19	Field, postspawning	24.7±6.36 $n = 14$	24.9±6.35 $n = 15$	>.1
Aug. 27	Field, postspawning	18.2±4.44 $n = 10$	19.3±4.51 $n = 10$	>.1
July 8	Captive 1 yr, prespawning	15.5±3.60 $n = 8$ (15.3±6.12)	8.71±3.67 $n = 7$ (5.4±2.71)	<.01
Aug. 1–14	Captive 2 yr, postspawning	8.5±3.12 $n = 10$	9.6±3.23 $n = 10$	>.1

activity and liver-somatic index had declined about 40% (Table 2).

Attempts were made to establish correlations of both uninduced and induced specific activity with body and liver weight. The fish were placed in two 270-L tanks with 1%/min water turnover; 200 mL of oil was added to one tank and the fish exposed for 8 d before liver removal. Linear regressions of PPO hydroxylase specific activities against body and liver weights revealed no significant correlation (Table 3). Size selection when sampling was therefore not of critical importance.

HYDROXYLASE INDUCTION BY EXPOSURE IN WATER

Preliminary experiments established the amount of oil necessary to maintain the animals in an induced state and to create oil concentrations within the sensitivity range of the fluorescent measuring procedure; 200 mL crude oil on 270 L seawater with 1% water exchange per minute was sufficient. The measured levels of oil were within the ranges generally associated with oil spill incidents (McAuliffe 1977), namely 0.2–2 mg/L (Fig. 1).

BP hydroxylation was rapidly induced by oil exposure (Fig. 1). Specific activity followed fluctuations in oil concentration, and significant ($P < 0.05$) induction persisted for a week following the end of exposure. A similar pattern was observed when PPO hydroxylation was measured on the same extracts. The ratios of induced to control activities were smaller with PPO, with the result that at some time points (days 5, 9, and 15), they did not meet the test of significance. In cunners, the levels of waterborne oil observed in this experiment seem to represent the limits of sensitivity of the method using the PPO substrate.

TABLE 2. Effect of 8-wk starvation on specific activity of uninduced hepatic AHH. Liver-somatic indices (liver wt/body wt × 100) were also measured. The experiment was conducted in September and October 1977 when no sex differences in enzyme activity or liver-somatic index were detectable. Specific activities are expressed as the mean ± SD in units defined in Materials and Methods.

Sample	Specific activity		Liver-somatic index
	PPO hydroxylation	BP hydroxylation	
Fed ($n = 20$)	10.3±2.30	9.3±2.88	2.6±0.68
Starved ($n = 20$)	6.1±2.53	4.7±2.45	1.3±0.21
Probability *P* of null hypothesis	<.01	<.01	<.01

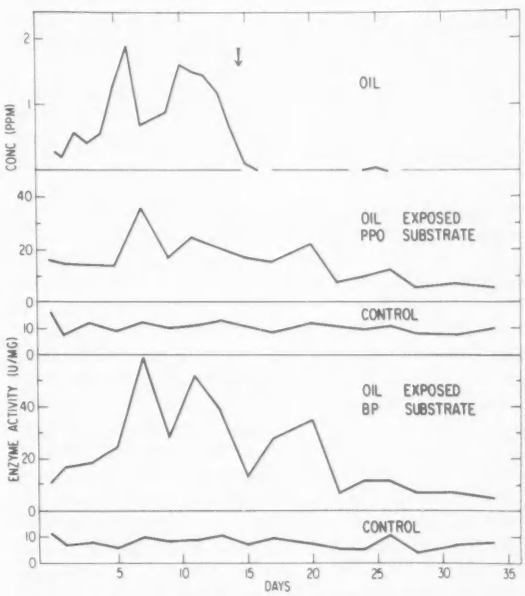

FIG. 1. Induction of two AHH activities by crude oil. Oil concentrations were measured in the overflowing water. Each concentration shown is the moving average of three concentrations (before, at, and after the time shown). Each enzyme specific activity point (fluorescence units/mg protein) represents the average of five fish, except that four fish were sampled from the control group after day 24. Oil exposure was ended at the time indicated by the arrow. Error bars are omitted for clarity (see text).

TABLE 3. Correlations of specific activity of PPO hydroxylation with body and liver weights of cunners.

Correlation	Wt range of body or liver (g)	n	r	P
Uninduced AHH vs. body wt	95–660	29	−0.29	>0.1
Uninduced AHH vs. liver wt	1.5–9.0	29	−0.09	>0.1
Induced AHH[a] vs. body wt	85–645	36	−0.03	>0.1
Induced AHH vs. liver wt	0.5–12.0	36	−0.07	>0.1

[a]Induced by 8-d exposure to a surface slick of crude oil.

TABLE 4. Induction of specific activity of hepatic AHH by feeding crude oil or mussel tissue contaminated with oil. Experiments were conducted in August and September 1977, when sex differences in activity were not detectable. Data are shown as mean ± SD in units defined in Materials and Methods.

Force-feeding treatment	PPO hydroxylation	BP hydroxylation
Salt water (n = 7)	5.2±1.40	—[a]
Crude oil (n = 14)	17.7±9.16[b]	—
Uncontaminated mussel tissue (n = 11)	5.1±1.66	3.8±1.81
Contaminated mussel tissue (n = 12)	25.9±9.29[b]	72±26.5[b]
Not force-fed (n = 8)	5.5±2.30	—

[a]Not measured.
[b]Differences between oil-exposed and corresponding control, $P < .001$.

HYDROXYLASE INDUCTION BY GASTROINTESTINAL EXPOSURE

Groups of fish were force-fed either 0.3 mL salt water or 0.1 mL crude oil and placed in the compartmented (rapid-washout) tank. The oil-fed fish showed a greater than threefold induction over controls after 1 wk (Table 4). Untreated animals and those fed salt water did not differ in activity from each other.

Fish fed 1–1.5 g oiled mussel tissue at 48-h intervals demonstrated an increase of greater than fivefold after 2 wk, compared with those fed clean mussel tissue (Table 4). The oil content of the mussel tissue was about 500 mg/kg, and the synchronous excitation–emission fluorescence spectrum of oil extracted from the tissues was indistinguishable from that of the oil used to contaminate the mussels (Fig. 2).

RELATIONSHIP OF BENZOPYRENE AND DIPHENYLOXAZOLE HYDROXYLATION

The substitution of PPO for BP in the AHH assay permits large numbers of assays to be performed without precautions necessary in the handling of BP. PPO has been shown to be nonmutagenic in the Ames bacterial mutation assay both with and without microsomal activation (J. F. Payne and R. Maloney, these laboratories, personal communication). At moderate levels of induction the specific activities of induced and uninduced homogenates toward the two substrates were positively correlated (Fig. 3); above a certain activity the induction toward PPO seemed to saturate. Whenever they were used together in an experiment throughout this work, the qualitative results were similar (e.g. Fig. 1). Moreover, the fluorescent PPO product was

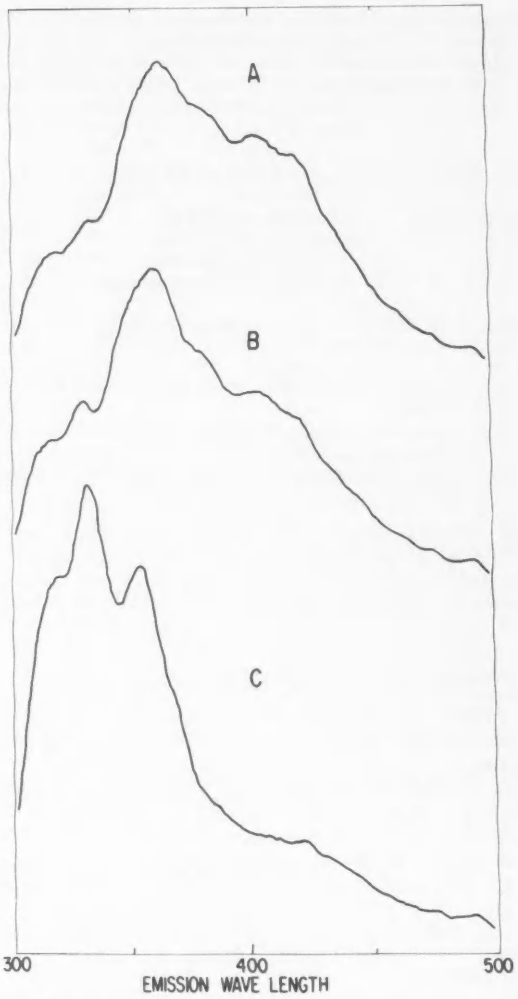

FIG. 2. Fluorescence scans of isooctane extracts of mussel tissue. Excitation and emission wavelengths were scanned simultaneously with a constant difference of 27 nm. A, Crude oil; B, extract of oil-contaminated mussel tissue; C, uncontaminated mussel tissue. Method of Hargrave and Phillips (1975).

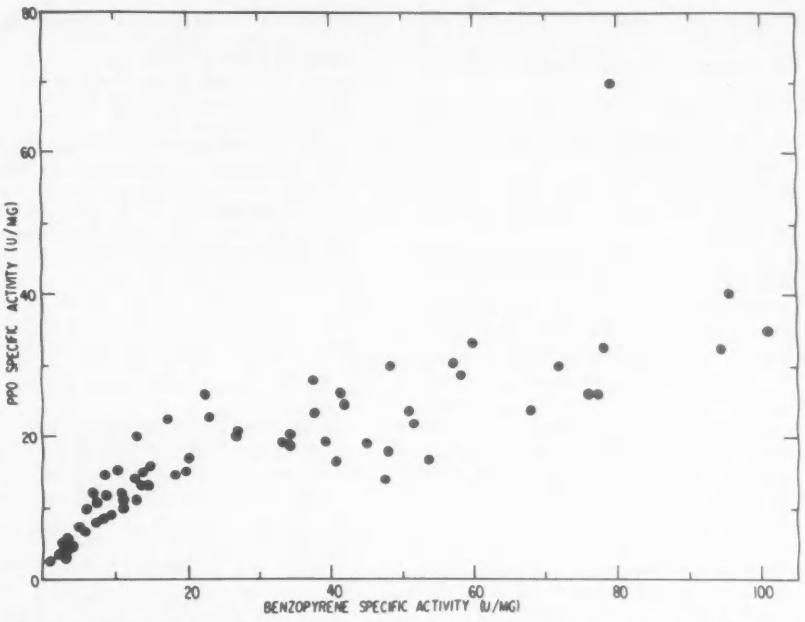

FIG. 3. Plot of specific activities of extracts toward PPO and BP as substrates. Points were pooled from several experiments and represent oil-induced as well as uninduced fish.

insensitive to fluorescent room lighting for over 50 h of continuous exposure, unlike the BP product which decomposed at a significant rate.

Discussion

The following characteristics have been established as guidelines to the use of the cunner as a monitoring animal for aryl hydrocarbon hydroxylase activity:

a) Cunners remain in a relatively small home range throughout their adult lives. Because of their winter torpor (Green and Farwell 1971), sampling is not practical at water temperatures below 6°C without the use of divers.

b) Female fish should be rejected from the sample. If necessary, females may be acceptable after the time of spawning (July in Newfoundland).

c) Since starvation can influence AHH specific activities somewhat, it would be prudent to monitor liver-somatic indices while sampling, and to reject samples or sampling locations where abnormal liver sizes are observed. However, uninduced specific activities can be unchanged by 5-wk starvation (Fig. 1). It is therefore unlikely this precaution will result in frequent rejections of field measurements.

d) The level of enzyme induction tracks oil concentrations with a delay of 1 or 2 d. Induction of AHH, therefore, reflects the current state of oil contamination under these circumstances. In trout and capelin, induction requires up to 2 wk (Payne and Penrose 1975a), and in trout persists 2 wk after exposure (W. R. Penrose and L. L. Dawe unpublished data). These species may yield a "historical" record of oil contamination, allowing detection of a spill some time after the oil has disappeared.

e) Petroleum served as an inducer whether accommodated in ambient water, ingested directly, or incorporated into ingested food. Bivalves, a common item in the diet of cunners, cannot metabolize polycyclic hydrocarbons (Lee et al. 1972; Payne 1977). They accumulate oil to high levels and lose it very slowly (Vandermeulen and Penrose 1978). Although cunners recover very quickly from oil exposure, one of the major components of their diet does not, and can serve as a reservoir of the inducing fractions of oil.

f) The substitution of PPO for BP makes AHH monitoring a safer and more practical undertaking for the routine or monitoring laboratory. The relationship is not ideal (Fig. 1 and 3); likely PPO and BP share two or more cytochromes P450 with overlapping substrate specificities. (The phenomenon of overlapping specificities is exemplified in the work of Guengerich 1977.) In this sense, the term "aryl hydrocarbon hydroxylase" is strictly an operational definition, so it is legitimate to propose PPO, a heterocycle, as a substrate for AHH.

Distinct from the substrate specificity of the induced cytochromes, the induction mechanism itself exhibits specificity. The best-studied example of this is the specific induction of benzphetamine- and benzopyrene-

specific cytochromes in rat liver (Ryan et al. 1975). Payne and Penrose (1975b) demonstrated induction of BP hydroxylation in trout by oil and oil refinery effluent, but not by polychlorinated biphenyls or representative organochlorine, organophosphate, or carbamate pesticides. Selectivity against nonpetroleum potential inducers has yet to be established in cunners. In most pollution situations, however, the nature of the pollutant is either immediately apparent or can be confirmed by chemical analysis.

The AHH method has immediate value in monitoring for several reasons. Foremost are its simplicity, speed, economy, and sensitivity (Penrose 1978). It may be surprising to those unfamiliar with the trace analysis of petroleum that there is yet no consensus on any single, fully satisfactory method of chemical measurement (e.g. Zsolnay 1978). Reliable analysis must involve an intelligent choice among infrared, ultraviolet, fluorescent, gas-chromatographic, and mass-spectrometric methods (Clark and Brown 1977). Since AHH measurement involves a physiological response to petroleum, and physiological responses are usually the primary concern of those involved in hydrocarbon monitoring, we feel that it will find its greatest value as a complement to chemical analysis.

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The Lake Washington Ecosystem: The Perspective from the Fish Community Production and Forage Base[1]

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In Lake Washington, fish production through detritus-based food chains is substantially greater than fish production through the grazing food chain. The lack of significant grazing by fish on the zooplankton is a consequence of both piscivore predation and conditions in the planktivore spawning environment. At low planktivore abundance, squawfish may switch to benthos feeding, exploiting the abundant prickly sculpin. At high planktivore abundance, squawfish feed more heavily on planktivores. Thus, even when reproductive success of planktivores is good, swamping of the squawfish population does not occur and depensatory mortality due to squawfish predation prevents planktivore abundance from increasing to the point where zooplankton resource depletion would occur. Benthic–littoral species are vulnerable to predation essentially only as larva and juveniles. They avoid predation by occupying littoral and epibenthic refugia. Recruitment to the adult population from these refugia may be sufficient to account for the greater rate of benthos exploitation by fish relative to the rate of zooplankton exploitation by fish. *Neomysis* is an important component of the Lake Washington fish production, since potentially *Neomysis* is a regulating agent on the zooplankton, and reduction in *Neomysis* predation on zooplankton, due to decreasing abundance and a deeper vertical distribution, may be partly responsible for the recent reappearance of *Daphnia*. The response of the fish community to trophic changes in Lake Washington has been slight. No consistent trends in the growth of fish utilizing zooplankton were observed. However, annual growth increments of consumers utilizing the benthic detrital food chain have declined with sewage diversion. The insights gained from analyzing the Lake Washington fish community structure and the Lake Washington carbon budget corroborate the above response of the fish community to trophic changes. Planktivores are predator-controlled and not able to deplete zooplankton resources, and thus would be insensitive to alterations in standing crop of zooplankton. On the other hand, benthic–littoral fish are more resource-limited and would be expected to respond to alterations in their forage base.

Key words: ecosystem, fish, production, Lake Washington, eutrophication, predation

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Dans le lac Washington, la production de poissons par l'intermédiaire des chaînes alimentaires à base de détritus est beaucoup plus forte que celle que donne la chaîne alimentaire à base de broutage. Le fait que les poissons ne broutent pas à un degré significatif le zooplancton est le résultat tant d'une prédation sur les piscivores que des conditions de l'environnement reproducteur des planctivores. Quand les planctivores sont peu abondants, la sauvagesse peut changer et adopter un mode d'alimentation benthique, se nourrissant de chabots visqueux abondants. Quand les planctivores sont abondants, la sauvagesse mange davantage de planctivores. C'est pourquoi, même quand les planctivores ont une reproduction réussie, il n'y a jamais submersion de la population de sauvagesses et la mortalité anticompensatoire causée par la prédation des sauvagesses empêche les planctivores d'augmenter au point où la ressource zooplanctonique s'épuise. Ce n'est qu'aux stades de larves et de jeunes que les espèces bentho–littorales sont vulnérables à la prédation. Elles évitent les prédateurs en occupant des refuges littoraux et benthiques. Les recrues qui quittent ces refuges pour se joindre à la population adulte peuvent suffire à expliquer le taux plus élevé d'exploitation du benthos par les poissons comparativement à leur taux d'exploitation du zooplancton. *Neomysis* est un composant important de la production de poissons du lac Washington, car l'espèce est un agent possible de régulation du zooplancton et il se peut qu'une diminution de prédation de *Neomysis* sur le zooplancton, par suite d'une abondance moindre et d'une distribution verticale plus en profondeur, soit responsable de la récente réapparition de *Daphnia*. La communauté ichtyologique n'a que très peu réagi aux changements trophiques qui se sont produits dans le lac Washington. Nous n'avons observé aucune tendance régulière dans la croissance des poissons se nourrissant de zooplancton. Cependant, les augmentations annuelles de croissance des consommateurs se nourrissant à même la chaîne alimentaire à base de détritus benthiques ont diminué avec le détournement des eaux usées. L'analyse de la structure de la communauté ichtyologique du lac Washington et du budget du carbone de ce lac est en accord avec cette réponse de la communauté ichtyologique aux changements trophiques. Les planctivores sont contrôlés par les prédateurs et ne peuvent épuiser les ressources zooplanctoniques, et seraient ainsi insensibles aux changements dans la biomasse de zooplancton. D'autre part, les poissons bentho–littoraux sont plus limités par la ressource et l'on s'attendrait qu'ils réagissent à des changements dans la biomasse des organismes fourrage.

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THIS paper presents the Lake Washington ecosystem from the perspective of total fish community production and the respective contributions of forage base groups of zooplankton, mysids, benthos, and fish to this production. The objective is to provide insight into the response of ecosystem components to changes in lake trophic state and into the determinants of fish community structure. This study provides information for comparison with other ecosystems of differing trophic states and perturbational histories. Loftus and Regier (1972) have suggested that comparative approaches are useful because they provide contrasts for drawing and testing inferences regarding fish community response to stressed and unstressed conditions. Lake Washington is particularly suited for ecosystem studies because of its unique perturbation history. Lake Washington is a lowland mesotrophic lake lying adjacent to Seattle and is well known as a case history in eutrophication and subsequent recovery after diversion of treated sewage (Edmondson 1972a, b, 1974a, 1977; Chasan 1971).

Study Area

Lake Washington is a warm monomictic lake. Stratification occurs from June through October, and the thermocline is typically located in the 10–20-m interval. Surface water temperatures range from 4 to 6°C in winter to over 20°C in summer. Physical characteristics of Lake Washington are summarized in Table 1.

Two major tributaries flow into Lake Washington. The Cedar River entering the lake at the south end contributes 55% of the inflow, and an additional 35% is furnished by the Sammamish River at the north. Several smaller streams contribute another 10% of the water income. Prior to 1916, the main inflow to Lake Washington was through the Sammamish River and outflow was through the Black River to Puget Sound. With construction of the Chittenden Locks and the Lake Washington ship canal, joining Lake Washington and Puget Sound through Union Bay and Lake Union, additional water was needed for operation of the locks. Accordingly, the Cedar River was diverted into Lake Washington and the original outlet was blocked.

Residential development has occurred along most of the 115-km shoreline. Bulkheads and docks have altered these areas, with the exception of areas designated as parks and the shorelines with wide littoral areas. The lake has shallow areas in bays and river mouths, but most shore areas are relatively steep.

There are 29 resident or transient species of fish found

TABLE 1. Physical characteristics of Lake Washington (from Anderson 1954 unless otherwise indicated).

Maximum depth (m)	65
Mean depth (m)	33
Area (km^2)	87.6
Volume (km^3)	2.88
Length (km)	35.1
Mean width (km)	2.4
Elevation (m)	4.3
Turnover rate of lake volume (yr^{-1})	2.9
Net sedimentation rate for 1958–74 ($mm \cdot yr^{-1}$)[a]	5.3

[a]Birch (1976).

in Lake Washington (Wydoski 1972). Wydoski lists the following 12 resident fish species as either common or abundant: prickly sculpin (*Cottus asper*), juvenile sockeye salmon (*Oncorhynchus nerka*), peamouth (*Mylocheilus caurinus*), northern squawfish (*Ptychocheilus oregonensis*), yellow perch (*Perca flavescens*), longfin smelt (*Spirinchus thaleichthys*), threespine stickleback (*Gasterosteus aculeatus*), largescale sucker (*Catostomus macrocheilus*), brown bullhead (*Ictalurus nebulosus*), black crappie (*Pomoxis nigromaculatus*), largemouth bass (*Micropterus salmoides*), and carp (*Cyprinus carpio*).

The first seven species in this list are the most common and their abundance, annual production, and diet are dealt with here. The last four species are relatively restricted, being found in weedy bays and undeveloped shoreline that constitute only a small portion of the total fish habitat of Lake Washington because of urbanization and shoreline development (Hockett 1975). Suckers are a long-lived, slow-growing species that consume only benthos (Scott and Crossman 1973) and are common throughout the lake. Large-scale suckers are less abundant than squawfish and are a minor component of the total fish production of the lake (Bartoo 1972).

Materials and Methods

All fishing methods were selective with respect to both size of fish and habitat sampled. To obtain comparable population statistics for all age-classes of several species of fish, it was necessary to use several pieces of gear, and to obtain the catchability coefficient, selectivity, and the size or age at which fish were fully recruited for each type of sampling apparatus.

A long-term sampling program was not undertaken specifically to monitor the response of several populations to trophic changes in Lake Washington. Instead, we utilized the results of several diverse studies, most of which were individual efforts, for estimates of the abundance of each age-class of the major fish species in Lake Washington. Then we assessed the fish populations quantitatively in terms of annual production, growth, and prey consumption rates.

This study summarizes and synthesizes the work of many people over the years 1962–76. Three sampling methods were used.

LIMNETIC SAMPLING

Limnetic sampling with midwater trawls and hydroacoustic gear was targeted at juvenile sockeye salmon, longfin smelt, and threespine stickleback. The limnetic fish populations in Lake Washington have been sampled since 1962 (Dryfoos 1965; Woodey 1971; Dawson 1972; Traynor 1973; Doble 1974; Moulton 1974). Acoustic estimation techniques have evolved over this period (Thorne 1970, 1971, 1972, 1973; Thorne and Lahore 1969; Thorne and Woodey 1970; Thorne et al. 1972, 1974). Also, population estimates can be derived solely from the trawl catch per unit effort (Traynor 1973).

Catches from midwater trawl hauls were used to determine length (fork length for sockeye, and standard length for stickleback and smelt), weight, and species composition (used in conjunction with acoustic surveys). During the years 1967–71, trawl surveys were incomplete. The catches from those strata not sampled were considered as missing data and were estimated by simple linear regression from those strata sampled. The population estimates presented here are simple averages of all point estimates (from acoustic as well as net sampling) made December through January when the limnetic fish were fully recruited to the gear.

Neomysis awatchensis were caught in substantial numbers during the nocturnal sampling with the Isaacs–Kidd midwater trawl (IKMWT). A 2-m IKMWT was used during the early period May 7, 1962 to October 21, 1964, and a 3-m IKMWT thereafter. To standardize these catch data, an effective cross-sectional area for the two nets was estimated using information from Banse and Semon (1963) and Friedl (1971). The population estimation technique for *Neomysis* was patterned after the net estimation technique for limnetic fish (Traynor 1973). Missing data due to incomplete trawl surveys were similarly estimated.

The diet composition of limnetic fish species in Lake Washington was determined from diel sampling at roughly 2-mo intervals, November 1974–October 1975. Sampling methods and means of determining numerical diet composition are given in Doble and Eggers (1978). The mean body carbon content for each prey species found in the diet was determined by measuring the mean length of each prey species and then converting that length to total body carbon from relationships given by M. L. Perkins (Water and Air Resources, Dept. Civil Engineering, Univ. Washington, Seattle, Wash., personal communication). Using this information, we converted the numeric diet composition to diet composition by prey body carbon content. This analysis was performed on individual fish stomachs. Stomach contents were pooled by fish age-class and sampling date and then averaged to give mean diet composition by prey body carbon content.

GILLNET SAMPLING

Gillnet sampling was targeted at peamouth, squawfish, and yellow perch. The primary gear used for sampling these species was monofilament gill nets. Panels of mesh from 2.54 to 12.70 cm, in 1.27-cm increments, were connected in random order to form the nets. Gill nets were fished in either a horizontal or a vertical mode. Details of the horizontal gillnet construction are given by Nishimoto (1973) and Hansen (1972). Horizontal gill nets sample the stratum within 1.83 m of the bottom. Vertical gill nets sampled the entire water column. Details of the vertical gillnet construction are given in Hansen (1972), Bartoo 1972), and Bartoo et al. (1973). Data collected consisted of standard life history information — length, weight, sex, gonad weight, otolith or scale sample, and stomach sample.

Population estimates based on the horizontal and vertical gillnet sampling were given by Bartoo (1977). The estimated abundance of age 1+ peamouth from limnetic

sampling was extrapolated to population estimates of peamouth, northern squawfish, and yellow perch from information on relative abundance; horizontal, vertical, and regional distribution; age composition; and age structure from gillnet catches. The gillnet catch data were adjusted for selectivity by a procedure modified from Hamly (1975) using data given by Hansen (1972). Abundances of age 0+ peamouth, age 0+ and 1+ squawfish, and 0+ yellow perch, not yet recruited to the gillnet sampling gear, were extrapolated from the abundance of older age-classes based on rate of natural mortality.

Baited Minnow Trap Sampling

Sampling with baited minnow traps was targeted at prickly sculpin. Largescale sucker fillets were used as bait. Data from this sampling consisted of standard life history information — length, weight, sex, gonad weight, otolith sample, and stomach sample.

Population estimates based on the baited minnow trap sampling are also given by Rickard (1978). Rickard determined the mean trapping area of each trap by an experiment in which strings with traps at various distances apart were fished. The CPUE increased asymptotically as the distance between traps increased allowing estimation of mean trapping area. The catches were adjusted for selectivity using a model described by Rickard (1978) and then extrapolated to a population estimate using the mean trapping area and area of the particular stratus fished.

Growth, Production, and Biomass

Seasonal growth curves by weight for sockeye, smelt, and stickleback were estimated from limnetic sampling. Sample sizes were insufficient for directly constructing seasonal growth curves for all age-classes of squawfish, peamouth, yellow perch, and prickly sculpin. However, the mean annual growth increments (in length) for all constituent age-classes were determined for peamouth (Nishimoto 1973), squawfish (Olney 1975), yellow perch (Nelson 1977), and sculpin (Rickard 1978) by the back-calculation method of determining mean length at annulus formation from growth zones on scales or otoliths (Tesch 1971; Chugunova 1963). For some year-classes, sample sizes were sufficient for direct estimation of seasonal growth curves by length or weight. The monthly growth increments in length or weight were converted to percentage of the annual growth increment. Bartoo (1977), Rickard (1978), and Nelson (1977) found no difference in the seasonal growth pattern expressed as percentage of annual growth increment for the following groups:

1. All age-classes of peamouth (weight).
2. Age 2–4 squawfish (immature) (length).
3. Age 5 and older squawfish (mature) (length).
4. Age 2 and older yellow perch females (mature) (length).
5. Age 2 and older yellow perch males (mature) (length).
6. Age 1+ yellow perch (immature) (length).
7. All age-classes of prickly sculpin (weight).

The data for each of these groups were pooled to give a curve of monthly growth increments. From this information and the mean annual growth increments a seasonal growth curve for the above age-classes and species was computed. Seasonal growth curves were not available for age 0+ and 1+ squawfish and age 0+ yellow perch. For those groups growth was assumed to be linear. If the measured monthly growth increments were in units of length, the derived seasonal growth curve (in units of length) was converted to units of weight via length–weight relationships given in Olney (1975) and Nelson (1977). If the measured monthly growth increments were in units of weight, the annual growth increments from scale studies were converted to weight based on the technique of Pienaar and Ricker (1968) and weight–length relationships given by Nishimoto (1973) and Rickard (1978).

Production is defined here as the total amount of tissue elaborated in the population or community under study in a given period of time (Allen 1971). That is,

$$P = \int_{T_1}^{T_2} N_t \frac{dW_t}{dt}\, dt \tag{1}$$

where P is the production, T_1 is the beginning of the time period, T_2 is the end of the time period, N_t is the number of fish in the population at time t, and dW_t/dt is the instantaneous rate of growth in weight. To compute production, a model is needed for abundance (N_t) and a model for growth (W_t). From analyses of catch curves, Bartoo (1977) found mortality to be an exponential decay function for peamouth, squawfish, and yellow perch. Similar results were found for sculpin (Rickard 1978) and juvenile sockeye (Bryant 1976). Thus,

$$N_t = N_o \exp(-mt) \tag{2}$$

where m is the instantaneous rate (month^{-1}) of natural mortality. To simplify the computation of annual production, the year was divided into monthly intervals where growth was linear; hence dW_t/dt is constant during those intervals. Substituting equation (2) into equation (1) and integrating yields

$$P = \sum_{i=1}^{12} \Delta W_i N_i \left[\frac{1 - e^{-m}}{m}\right] \tag{3}$$

where ΔW_i is the monthly growth increment and N_i is the population abundance at the beginning of month i. P was computed for each species and constituent age-class. Mean annual biomass (B) was similarly computed for each species and constituent age-classes:

$$B = \frac{\sum_{i=1}^{12} W_i N_i \left[\frac{1 - e^{-m}}{m}\right]}{12} \tag{4}$$

where W_i is the mean weight during month i.

Results

Particulate Organic Carbon Budget

To relate the Lake Washington fish community to the trophic economy by the lake, we estimated the dietary components of the annual fish production. To make this estimate we had to construct the annual pattern of abundance, growth, and diet for each major fish species and respective age-class.

Mean annual biomass and production of the limnetic species were computed for the period January 1, 1972

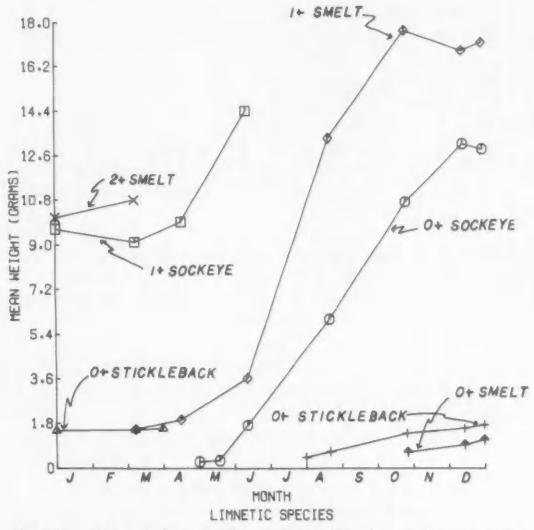

FIG. 1. Seasonal growth trajectories for relevant year-classes of the limnetic fish species in Lake Washington during 1972.

to December 31, 1972. In Lake Washington, threespine stickleback and longfin smelt mature at age 1 and age 2, respectively, and die after spawning. This period encompassed the growth (Fig. 1) of 1970 and 1971 year-classes of juvenile sockeye salmon (migrated spring 1972 and 1973, respectively); 1971 and 1972 year-classes of threespine stickleback (matured spring 1972 and 1973, respectively); and 1970, 1971, and 1972 year-classes of longfin smelt (matured late winter 1972, 1973, and 1974, respectively). Using the respective instantaneous rates of natural mortality (Table 2), the abundances of the limnetic fish species during this period were extrapolated from the winter abundance before maturity or outmigration of the 1970, 1971 year-class of juvenile sockeye salmon; 1971, 1972 year-class of stickleback; and 1970, 1971, 1972 year-classes of longfin smelt.

Data on abundance, growth, and diet of the benthic–littoral fish species were collected from 1971 to 1975. Population abundances were essentially point estimates (Fig. 2). Because these species are long-lived, and, except for squawfish, show no extensive variation in year-class strength (Fig. 2), the bias due to annual variation in abundance is negligible. The abundance of the youngest age-classes of peamouth, squawfish, and yellow perch not yet recruited to the gill nets was estimated by extrapolating from the abundance of the older age-classes, taking into account the instantaneous rates of natural mortality (Table 2). Growth was estimated by extrapolating size at annulus formation (Table 3) by monthly values of mean annual growth increments. Most of the production and biomass of fish in Lake Washington is prickly sculpin (Table 4).

TABLE 2. Instantaneous (day^{-1}) rate of natural mortality for Lake Washington fish populations.

Population	Mortality	Source
Juvenile sockeye		
1970 year-class	−0.00290	Bryant (1976)
1971 year-class	−0.00274	Bryant (1976)
Smelt	−0.00282	Avg of the sockeye mortality rates
Stickleback	−0.00282	Avg of the sockeye mortality rates
Peamouth	−0.00397	Bartoo (1977)
Squawfish	−0.00074	Bartoo (1977)
Yellow perch	−0.00156	Bartoo (1977)
Prickly sculpin	−0.00295	Rickard (1978)

TABLE 3. Mean weight (grams) at annulus formation for various species of fish in Lake Washington.

Age	Peamouth	Squawfish	Prickly sculpin	Yellow perch males	Yellow perch females
1	9	—	1.0	8.8	10
2	38	26	7.2	52	65
3	81	94	16	125	171
4	132	187	26	188	281
5	190	293	41	242	376
6	240	408	60	282	454
7	303	528	81	328	502
8	352	650	110		
9	408	773			
10		897			
11		1,021			
12		1,145			
13		1,269			
14		1,393			
15		1,517			
16		1,641			
17		1,765			
18		1,889			
19		2,013			
20		2,137			
21		2,261			
22		2,385			

A great number of prey items are available to Lake Washington fishes. To provide a simple picture of carbon flow through water column and benthic communities, as well as to avoid a confusing presentation involving tens of prey species, the prey items in the diet were grouped according to zooplankton, benthos, mysids, and fish (Fig. 3 and 4). The diet of age 2+ peamouth is strictly benthos (Nishimoto 1973; Shanbhogue 1976).

The relative contribution of the zooplankton, mysids, benthos, and fish prey items to fish production was estimated by grouping fish according to similar feeding habitat and diet composition (Table 5). These functional groups ranged from strictly limnetic fish feeding on zooplankton and emergent insects to strictly benthic

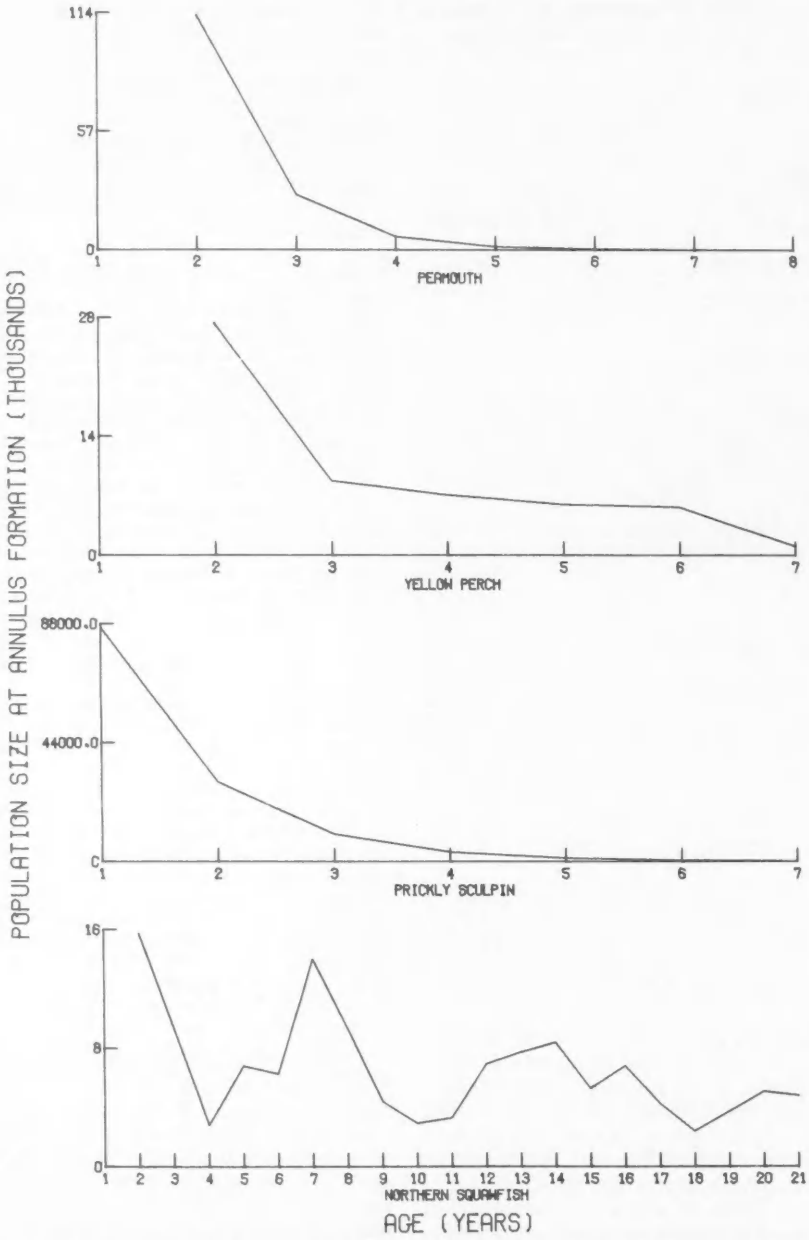

FIG. 2. Abundance at annulus formation for constituent age-classes of peamouth, yellow perch, prickly sculpin, and northern squawfish in Lake Washington.

feeding fish as evidenced by a diet of benthos, mysids, and bottom fish (sculpin). Older age-classes of sculpin were cannibalistic and can be considered piscivores as well as benthic feeders. The facultative piscivores (older age-classes of yellow perch and squawfish) feed in the water column as well as on the bottom.

The relative contribution of each prey group to fish production was estimated by partitioning the production

TABLE 4. Annual production and mean annual biomass of Lake Washington fishes.

Species	Annual production (kg wet wt/yr)	Percent of total production	Mean annual biomass (kg wet wt)	Percent of total biomass	Turnover rate $\frac{P}{B}$
Prickly sculpin	6.56×10^5	83.8	5.95×10^5	72.7	1.41
Juvenile sockeye salmon	4.88×10^4	6.2	4.07×10^4	5.0	1.19
Peamouth	2.65×10^4	3.4	1.98×10^4	2.4	1.34
Longfin smelt	2.68×10^4	3.4	3.07×10^4	3.8	0.87
Northern squawfish	1.55×10^4	2.0	1.16×10^5	14.2	0.13
Yellow perch	5.51×10^3	0.7	1.14×10^4	1.4	0.48
Threespine stickleback	3.42×10^3	0.4	4.53×10^3	0.6	0.75

of each constituent age–species class in the functional group by its respective diet composition and summing (Table 6). Of the prey groups, benthos contributed most (74.3%) and fish contributed least (6.4%) to fish production.

A particulate organic carbon budget incorporating the dietary components of fish production and ration was constructed for Lake Washington (Table 7). The Lake Washington carbon budget is incomplete because of the lack of data on littoral primary production and on allochthonous inputs to the lake. Data are also inadequate for estimating production, respiration, and diet of the *Neomysis* population. Values presented in parentheses reflect only the population cropped by fish and therefore serve as a minimum estimate.

The carbon budget shows that the benthic food chain is as important as water column processes to the trophic dynamics of Lake Washington, which is surprising for a deep lake where the littoral area is <20% of the lake surface area. However, fluvial and direct sedimentation inputs of carbon to the sediments appear insufficient to fuel the benthic production (Table 7). This deficiency was most likely due to unaccounted-for inputs of littoral production by periphyton and attached macrophytes.

In Lake Washington, cold littoral water sinking down the steep sides of the lake basin causes winter thermal convection currents (Syck 1964). These convection currents have been described as sufficient in magnitude to have eroded the original U-shaped Lake Washington basin to its present W shape (Gould and Budinger 1958). Thus, detrital material produced in littoral regions could be transported to profound regions of the lake.

Steele (1974) and Mills (1975) encountered imbalances in their analysis of the trophic economy of the North Sea ecosystem. They were unable to account for the observed demersal fish production from inputs to the demersal food web due to sedimentation of zooplankton fecal material if consideration was given to possible losses of bacteria respiration, metabolism of meiobenthos, and metabolism of carnivorous epifauna. At this time there are not enough studies of benthos and

TABLE 5. Definition of the functional groups of fish used to compute the relative contribution of zooplankton, benthos, mysids, and fish prey items to fish production.

Functional group	Fish species and age composition	Feeding behavior	Diet
Obligate planktivores	Age 0+ sockeye Age 1+ sockeye Age 0+ stickleback	Limnetic	Zooplankton and emergent insects
Smelt	Age 0+, 1+, and 2+ longfin smelt	Limnetic epibenthic	Zooplankton mysids, emergent insects
Facultative benthic	Age 0 to 2+ peamouth Age 0 to 1 squawfish Age 0 to 1+ yellow perch	Benthic epibenthic limnetic	Benthos, mysids, zooplankton
Obligate benthic	Age 2+ to 8+ peamouth Age 0 to 7+ sculpins	Benthic epibenthic	Benthos, mysids, sculpins
Facultative piscivores	Age 1+ to 6+ yellow perch Age 1+ to 21+ squawfish	Limnetic benthic	Benthos, mysids, fish

TABLE 6. Dietary components of fish production (numbers in parentheses are percentage total production).

Group	Biomass (kg wet wt)	Production (kg wet wt) per year)	Production due to forage items			
			Zooplankton	Benthos	Mysids	Fish
Obligate planktivores	45 200	52 200	47 640 (91.3)	4 110 (7.9)	450 (0.9)	0 (0)
Smelt	30 680	26 800	9 740 (36.3)	4 200 (15.7)	12 530 (46.8)	330 (1.2)
Facultative benthic feeders	19 610	24 460	12 000 (49.0)	11 890 (48.6)	580 (2.4)	0 (0)
Obligate benthic feeders	571 800	658 584	0 (0)	510 837 (77.6)	91 630 (13.9)	56 117 (8.5)
Facultative piscivores	127 700	19 420	0 (0)	2 790 (14.4)	2 060 (10.5)	14 570 (75.0)
Total	794 500	718 464	69 380 (8.9)	533 827 (68.3)	107 250 (13.7)	71 017 (9.1)

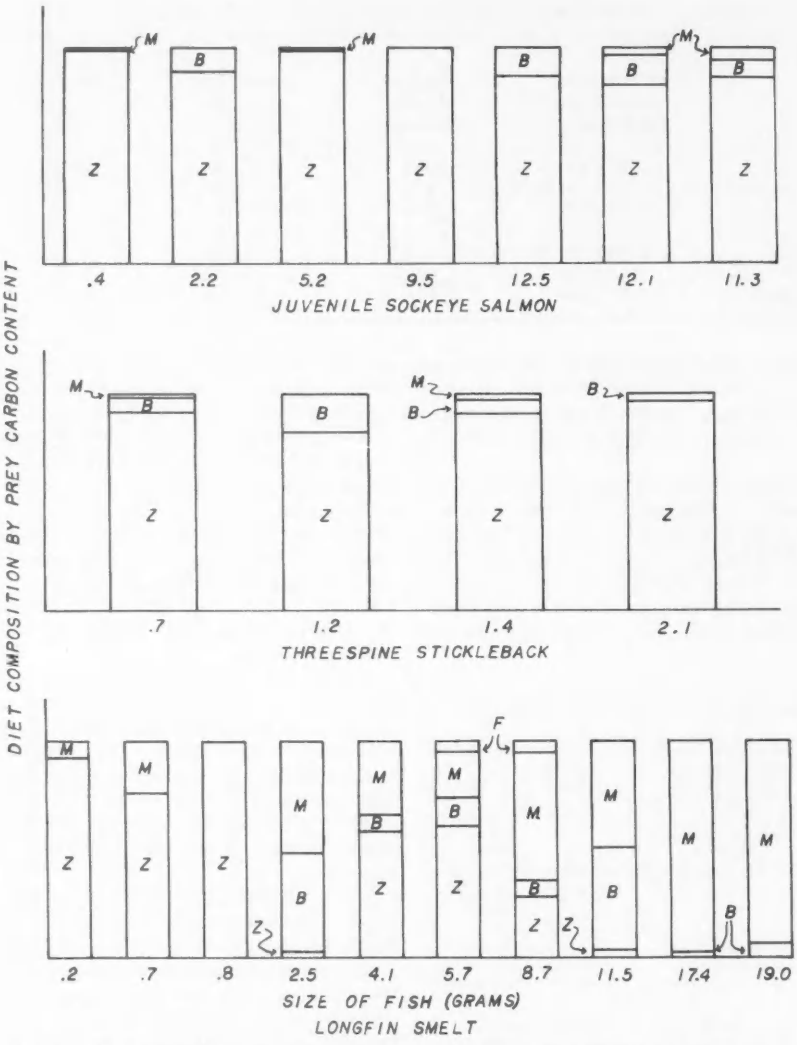

FIG. 3. Diet composition (by prey carbon content) for various sizes of juvenile sockeye, threespine stickleback, and longfin smelt in Lake Washington. These data reflect seasonal trends in diet as sampling was conducted over the period of limnetic residence for each species. The diet of sockeye (0.4–11.3 g) was collected February through February. Similarly, the diet of stickleback, (0.7–2.1 g) was collected August through February; age 0+ smelt (0.2–2.5 g) was collected August through February; and age 1+ smelt (4.1–19 g) was collected June through February. The component dietary items include zooplankton (Z), mysids (M), benthos (B), and fish (F).

zooplankton paralleling studies of fish production for generalization.

In Lake Washington the fish community is dominated by benthos feeders. The limnetic fish population was estimated to use only 1.7% of the annual zooplankton production. *Neomysis*, an organism that seemed unimportant in the catches from zooplankton sampling gear and midwater trawls, is potentially an important component of the water column food chains. In the limnetic zone of Lake Washington, *Neomysis* has declined in abundance since 1962 (Fig. 5). Abundance during 1968–71 was less than during 1974–75. The estimated mean biomass for *Neomysis* during the period November 5, 1974 to October 13, 1975 was 0.0144 g

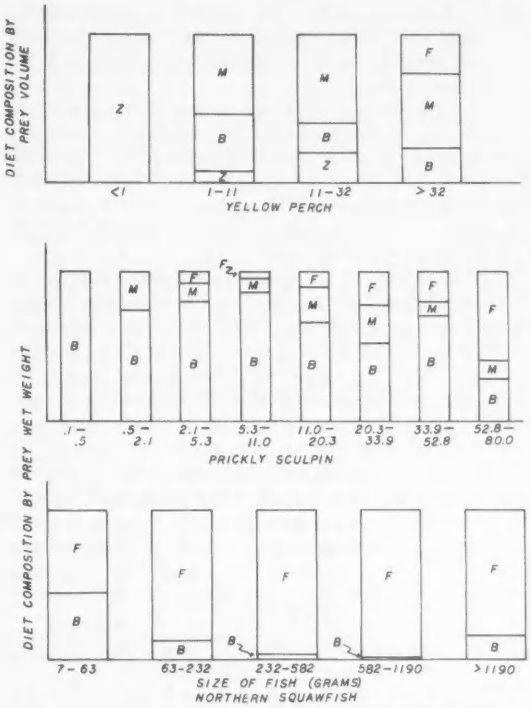

FIG. 4. Diet composition for various sizes of yellow perch (by prey volume), prickly sculpin, and northern squawfish (by prey wet weight) in Lake Washington. Data were pooled by size and do not reflect seasonal trends. The component dietary items include zooplankton (Z), mysids (M), benthos (B), and fish (F).

$C \cdot m^{-2}$. If it is assumed that the amount of *Neomysis* consumed by fish was the minimum *Neomysis* production during 1974, then the production/biomass (P/B) ratio was at least 90.3, an unreasonably high figure. The calculated P/B for Lake Washington zooplankton is 12.66. Mean zooplankton biomass during 1974 was estimated using unpublished zooplankton density (W. T. Edmondson, Dept. Zoology, Univ. Washington, Seattle, Wash., personal communication), mean length (Eggers and Doble unpublished data), and a conversion from length to body carbon content (Perkins personal communication). The high P/B for *Neomysis* indicates that we are underestimating the abundance of *Neomysis*. Accordingly, there may be sizable inshore and littoral populations not available to the sampling gear (Nelson 1977). Also, only a part of the population may be migrating from the bottom into the water column at night.

Fish consumed by yellow perch and prickly sculpin were small fish, mostly small prickly sculpin (Nelson 1977; Rickard 1978). Northern squawfish consumed both planktivorous fish (smelt, stickleback, and sockeye) as well as prickly sculpin.

Response of the Fish Community to Trophic Changes in Lake Washington

There were two periods of sewage input to Lake Washington. During the early part of this century, the lake received untreated sewage until diversion of the untreated effluent to Puget Sound was completed in 1936. This diversion was in response to health concerns as some communities used the lake for drinking water. Beginning in 1941, secondary sewage treatment plants dispersed effluent into Lake Washington. Because of public concern for the deterioration of the lake, diversion of the secondary treatment plant effluent began in 1963 and was completed by 1966. The phytoplankton community responded rapidly to the reduced nutrient loadings (Edmondson 1972a).

Specific components of the eutrophication history thus far documented are:

1. Nutrient loadings were 108 000 kg phosphorus in 1957; 231 000 kg in 1962; and 41 000 kg in 1974 (Edmondson 1977).

2. The summertime chlorophyll *a* concentration reached maximum levels (40 μg/L) in 1964, but were high from 1962 to 1966 (20–40 μg/L). Summertime Secchi disk readings were low (<1.5 m), 1962–67 (Edmondson 1972a).

3. Species composition of the algae has changed markedly since the period of maximum nutrient loading when filamentous blue-green algae constituted as much as 98% by volume of the phytoplankton. The percentage of blue-green algae has decreased sharply in recent years, constituting 44% of the phytoplankton in 1973 and 1974 (Edmondson 1977).

4. Zooplankton had shown no major changes in species composition until 1972 when *Daphnia* reappeared in the lake (Edmondson 1977). *Daphnia* had been observed in the 1930s (Sheffer and Robinson 1939) but not in the years 1950–72 (Edmondson personal communication). Some changes in abundance have occurred over the years but none that can be attributed to trophic changes in Lake Washington (Edmondson 1972b).

There was no consistent change in the size of juvenile sockeye at the end of the summer–fall growing season, 1966–75, that might be associated with change in the trophic condition of Lake Washington (Fig. 6). In stickleback, there was no consistent change between 1971 and 1975 in the size reached by December, even though stickleback increased greatly in abundance during the period 1967–76 while sockeye declined in abundance (Fig. 7).

Smelt exhibited cyclic abundance patterns for 1966–71 year classes, the even-numbered year-classes being more abundant than the odd-numbered year-classes. During these years, smelt exhibited density-dependent growth, the less abundant odd-numbered year-classes showing a higher growth rate (Fig. 6) than the even-numbered more abundant year-classes (Moulton 1974), a pattern that has disappeared in recent years. This pat-

tern of growth may be related to the long-term trends in abundance of *Neomysis* (Fig. 5), which is the major prey item of smelt older than age 1. During the period of density-dependent growth (1968–71), *Neomysis* abundance was very low.

Long-term patterns of growth were estimated for peamouth (Nishimoto 1973) and for squawfish (Olney 1975) by back-calculation techniques. Nishimoto showed that back-calculated annual growth increments increased from 1962 to 1967–68 when they peaked (Fig. 8). In subsequent years, a progressive decline in growth occurred. The maximum growth rates for peamouth were observed approximately 2 yr after maximum primary production resulting from cultural eutrophication (Edmondson 1972a). Olney (1975) compared the back-calculated total length at each annulus as well as annual growth increments during the first 5 yr of growth for 1955–71 year-classes of squawfish (Fig. 9). Annual growth increments during the first 3 yr of growth increased from 1955 to 1966–68 and declined thereafter. This pattern did not hold for the 4th and 5th yr of growth. Age 0–2+ squawfish feed primarily on benthos. The historical trends in growth of squawfish correlate with those of peamouth which also feed primarily on benthos.

Although there were trends of decreasing growth in fish utilizing benthos as food following sewage diversion, comparisons of size at annulus formation for squawfish (Olney 1975), peamouth (Nishimoto 1973), and yellow perch (Nelson 1977) show that the growth achieved by these Lake Washington fishes is greater than or equal to that in other lakes.

Although growth of Lake Washington planktivores has not changed during the period following sewage diversion, abundance has. Stickleback have increased greatly in abundance during 1967–76 while sockeye have declined (Fig. 2). The decline in sockeye abundance has been attributed to high incidence of midwinter floods during the last 7 yr in the Cedar River, washing the eggs out of the gravel (Bryant 1976; Miller 1976). The increase in stickleback abundance may be due to changes in littoral environment accom-

TABLE 7. Particulate organic carbon budget for Lake Washington. (All values are given in $g \cdot m^{-2} \cdot yr^{-1}$. See footnote for explanation of source data.[a])

Water column			Benthic–littoral		
Inputs	Value	Source	Inputs	Value	Source
Allochthonous			Water column		
Fluvial	20.0	1	Sedimentation	53.0	3
Precipitation	ND		Autochthonous		
Litter	ND		Periphyton	ND	
Autochthonous			Macrophytes	ND	
Phytoplankton production	157.0	2	Total inputs	53.0	
Total inputs	177.0				
Losses			Losses		
Outflow	0.5	1	Benthic respiration	52.0	8
Sedimentation	53.0	3	Fish respiration	2.0	6
Microplankton respiration	59.0	4	Burial	35.0	9
Zooplankton respiration	48.0	5	Emergence	ND	
Neomysis respiration	ND (2.4)	7	Macrophyte and periphyton respiration	ND	
Planktivorous fish respiration	0.5	6	Total losses	104.9	
Piscivorous fish respiration	0.03	6			
Total losses	163.0				
Internal transformations			Internal transformations		
Ingestion			Ingestion		
Material ingested by zooplankton	97.0	5	Material ingested by macroinvertebrates	113	10
Material ingested by *Neomysis*	ND (4.0)	7	Macroinvertebrates ingested by fish	3.1	6
Zooplankton ingested by fish	0.33	6	Fish ingested by fish	0.5	6
Neomysis ingested by fish	0.6	6	Production		
Fish ingested by fish	0.04	6	Microbial	ND	
Production			Macroinvertebrates	16.9	10
Microbial	ND		Fish production supported by macroinvertebrates	0.8	6
Zooplankton	19.0	5	Fish production supported by fish	0.1	6
Neomysis	ND (0.6)	7			
Fish production supported by zooplankton	0.10	6			
Fish production supported by *Neomysis*	0.15	6			
Fish production supported by fish	0.01	6			

panying trophic changes in Lake Washington. Stickleback are territorial and compete for suitable spawning substrate (Scott and Crossman 1973). During periods of peak nutrient loading, littoral areas of Lake Washington had mats of blue-green algae growing on the substrate (Chasan 1971). Possibly suitable spawning substrate or rearing habitat limited the Lake Washington stickleback population before 1970.

Zooplankton showed no consistent change in abundance or species composition from 1962 (Edmondson 1972b) until 1972 when *Daphnia* sp. appeared (Edmondson 1977). Large zooplankters present in Lake Washington include *Epischura nevadensis* and *Diaphanosoma* sp. before 1972, and *Epischura*, *Diaphanosoma*, and *Daphnia* after 1972.

Planktivorous fish in Lake Washington show extreme size-selective predation, but are not sufficiently abundant to regulate the large zooplankters. The reappearance of *Daphnia* in Lake Washington may have been a response to phytoplankton succession accompanying sewage diversion. However, in addition to planktivorous fish, there is another potential zooplankton predator, *Neomysis*, that is an important contributor to fish production in Lake Washington. Its biomass ingested by fish is twice that of zooplankton ingested.

The information we have on *Neomysis* is based on nighttime midwater trawls, and indicates that since 1962 *Neomysis* abundance has decreased and that the nocturnal vertical distribution has shifted to lower strata (Fig. 6). From 1962 to 1964, when lake water transparency was much lower than at present, substantial numbers of *Neomysis* were found in the water column during the day. Although we have no information on the present daytime vertical distribution, *Neomysis* must be near the bottom because they constitute a significant portion of the diet of prickly sculpin. This is because cottids are ambush predators, with no swim bladder, and therefore can feed effectively only near the bottom. The apparent downward shift in the vertical distribution of *Neomysis* may be a response to the changing ambient light conditions in Lake Washington as a consequence of sewage diversion.

The vertical distribution of *Neomysis* in Lake Washington is consistent with the behavior of a similar species, *Mysis relicta*. The vertical distribution of *M. relicta* in Lake Huron and Lake Michigan was strongly influenced by ambient light intensity (Beeton 1960). Beeton also found that *Mysis* were deeper in the water column on moonlit nights than on dark nights. Additionally, the introduction of *Mysis* into Lake Tahoe caused a virtual disappearance of *Daphnia* from that lake (Richards et al. 1975). Lasenby and Langford (1972) found that *Mysis* in Stony Lake was a benthic detritivore by day and a voracious carnivore preying on *Daphnia* by night.

These two pieces of evidence, the vertical distribution and the apparent decline in abundance of *Neomysis*, along with the information on *M. relicta*, suggest a second cause of the reappearance of *Daphnia* in Lake

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[a]1. Representative particulate organic carbon measurements in the Cedar and Sammamish rivers extrapolated from U.S.G.S. flow data (J. E. Richey, Fisheries Research Institute, Univ. Washington, Seattle, Wash., personal communication).

2. Phytoplankton production from ^{14}C uptake during 1974 (Devol and Packard 1978).

3. Losses of algal, fecal, and allochthonous material from the water column measured by sediment trap, March 1974 to March 1975 (Birch 1976).

4. Sum of euphotic and aphotic microplankton respiration during 1974 (Devol and Packard 1978). Respiration was measured by the activity of the respiratory electron transport system (ETS activity) (Packard 1971).

5. Net zooplankton respiration measured by ETS activity (Devol 1977). Based on summary data presented in Parsons and Takahashi (1973) and Edmondson (1974b), amount of material ingested assumed to be 2 times the respiration, and egestion was assumed to be 30% of ingestion.

6. Fish. The organic material ingested and respiration losses were estimated by simple energy budgets ($I = R + P + E$). All of the budget components are specified by gross conversion efficiency ($K = P/I$), the assimilation coefficient (α, $E = (1 - \alpha)I$), and the production (P); α was assumed to be 0.8 (Winberg 1956). Total body carbon was assumed to be 12.5% of wet weight. In the obligate planktivore, smelt, and facultative benthic functional groups, as well as age 0–1 sculpin (Table 5), K was assumed to be 0.3 (Eggers 1975). Because larger, older fish are less efficient in converting ingested material to growth (Winberg 1956), K for the obligate benthic (except age 0–1 sculpin) and facultative piscivores (except age 1+ to 21+ squawfish) was assumed to be 0.20. Squawfish are large, slow-moving top carnivores with even lower K. Age-specific respiration and egestion for squawfish were estimated using production (Table 4) and relationship of total metabolism to body size and ambient temperature given for cyprinids by Winberg (1956). These age specific estimates of I, R, and E for piscivores were attributed to water-column supported fish and benthos-supported fish based on diet composition. The whole lake production figures were converted to a per hectare basis by dividing by the surface area of the lake.

7. Minimum estimates (shown in parentheses) of ingestion, respiration, and egestion to support the production of *Neomysis* cropped by fish assumed that $I = 5P$, $E = 0.3\ I$, $K = 0.5\ I$. This budget is the same as that used for zooplankton.

8. Benthic respiration was measured for several profundal stations during September 1972 by Pamatmat and Bhagwat (1973). Since these samples were incubated at 10°C, it is necessary to convert to in situ temperature (mean annual water column temperature 15–58 m is approximately 8°C). The mean measured value of 600 kg C·ha^{-1}·yr^{-1} was converted to 520 kg C·ha^{-1}·yr^{-1} assuming a Q_{10} of 2.3 (Pamatmat 1971).

9. Permanent sediment burial given by Birch (1976).

10. Bissonnette (1975) gave production for Chironomidae, March 1973–March 1974. These numbers were converted from grams dry weight to kilograms carbon and multiplied by 2, since Thut (1969) found Chironomidae to constitute approximately one half of the benthos biomass. We assumed a 15% gross conversion efficiency to estimate the required food base of 1,130 kg C·ha^{-1}·yr^{-1}.

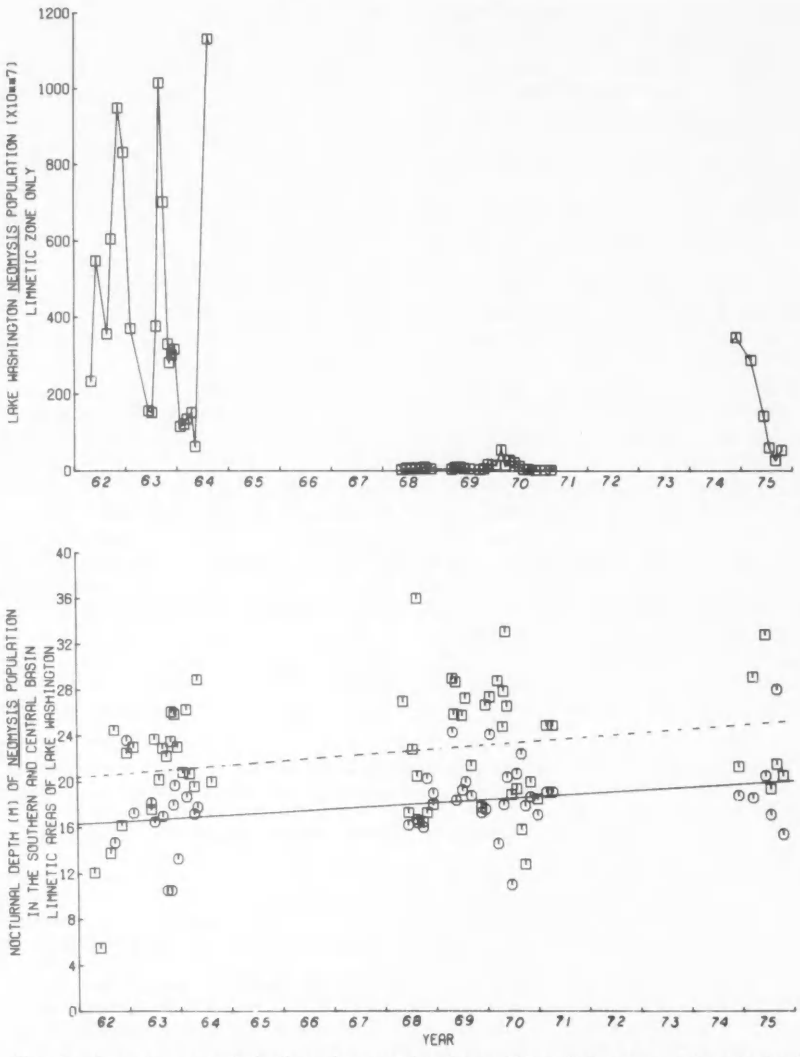

FIG. 5. Long-term trends in limnetic zone abundance (A) and the nocturnal mean depth of occurrence (B) of *Neomysis* in Lake Washington. Fitted linear regression line and data are plotted for the southern (○ solid line) and central (□ dashed line) basins. For the southern basin, $Y = 16.3 + 0.25X$, $R = 0.316$. For the central basin, $Y = 20.4 + 0.33X$, $R = 0.252$.

Washington. After the sewage diversion and subsequent decline in primary production, the amount of algae cropped by herbivorous zooplankton apparently remained constant because there was no decrease in zooplankton abundance associated with sewage diversion. Therefore, more organic material may have been reaching the sediments during past periods of high phytoplankton production than at present. Wissmar and Wetzel (1978) in a comparison of five temperate North American lakes showed that as primary production increased, a higher fraction was available to benthic and detrital food chains. If a decrease in benthos production resulted from sewage diversion, then the decline in *Neomysis* abundance may have resulted from fish switching from benthos to *Neomysis*. This decline in abundance coupled with the downward shift of the *Neomysis* distribution may create a "refuge" in the upper water column strata for prey organisms such as *Daphnia*. *Daphnia*, like other zooplankters, are much more abundant in the upper 20 m of the lake (W. T.

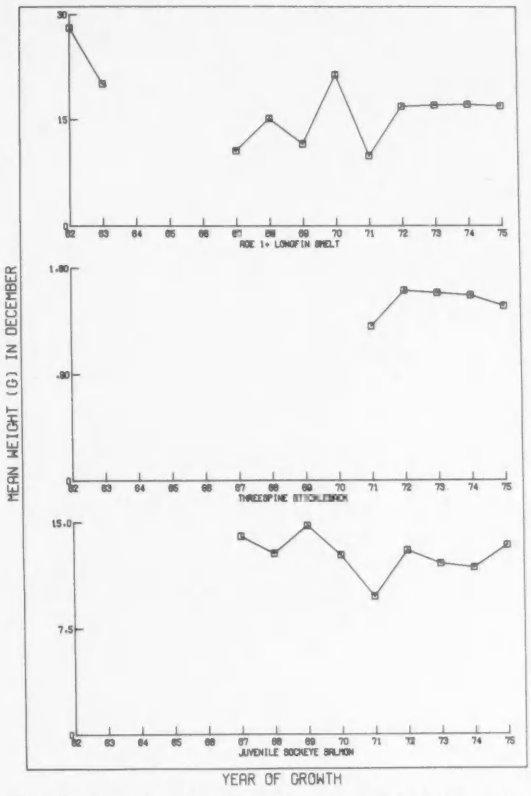

FIG. 6. Long-term trends in the mean weight in December for age 1+ longfin smelt, threespine stickleback, and juvenile sockeye salmon in Lake Washington.

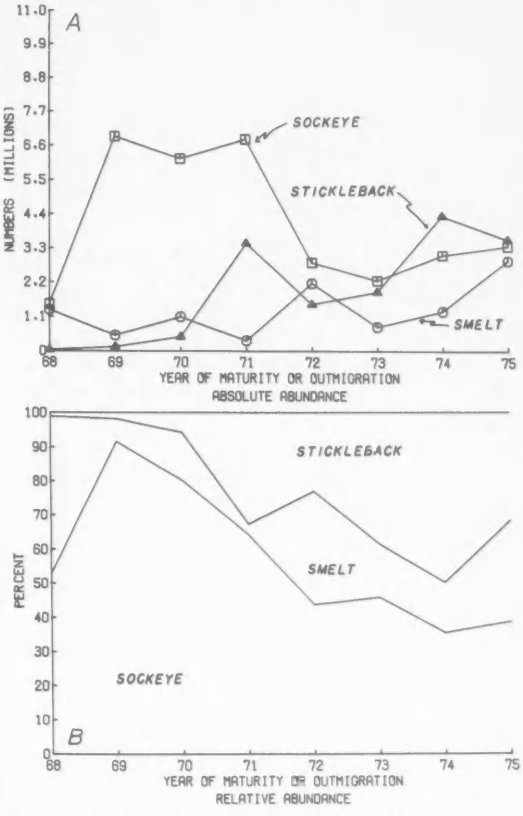

FIG. 7. Long-term trends in absolute (A) and relative (B) abundance of limnetic fish species in Lake Washington.

Edmondson personal communication). Thus, the limited evidence we have on both vertical distribution and abundance suggests that the magnitude of predation by *Neomysis* on the zooplankton community has declined since the early 1960s.

Lake Washington is unique as an experiment in eutrophication and subsequent oligotrophication with diversion of treated sewage. The response of the phytoplankton to the changing nutrient loading is well documented, but the response of Lake Washington higher consumers has not previously been documented. Detrimental effects of cultural eutrophication on salmonid communities occur at much higher nutrient loadings or more severe perturbations than occurred in the Lake Washington drainage basin (Colby et al. 1972). Detrimental effects result from depletion of hypolimnion oxygen or deforestation, erosion, damming, and pollution on the spawning tributaries.

Determinants of Limnetic and Benthic Fish Community Structure

The most significant result of this study is the determination that the fish community is dominated by benthos-consuming fish. This is surprising in a large deep lake where the area of the littoral zone is much smaller than the area of the limnetic zone. Furthermore, the magnitudes of benthos and zooplankton production are comparable (Table 7). If the prey resources were strictly limiting the fish populations, one would expect the magnitudes of benthos- and zooplankton-supported fish production to be more similar than observed in Lake Washington.

It is perhaps a truism to say that competition for resources and effects of piscivorous predation are the determinants of fish community structure. However, the structural manifestations of competition and predation are quite different and the structure of the Lake Washington fish community cannot be explained without consideration of the interaction of competition and predation.

Studies of morphological differences, habitat utilization, diet, and timing of feeding among cohabiting fish species in Lake Opinicon (Keast and Webb 1966; Keast 1970) and Lawrence Lake (Werner et al. 1977; Hall

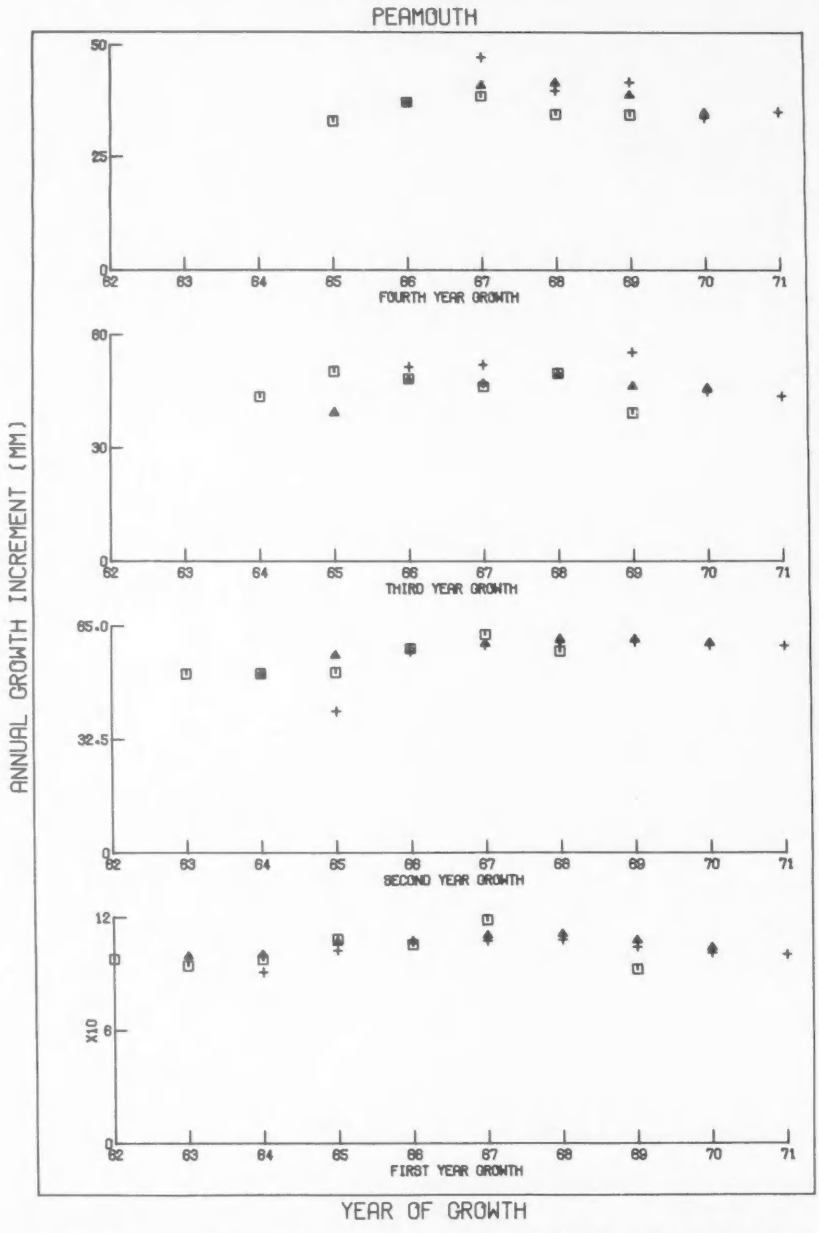

FIG. 8. Mean annual growth increments (mm) for each of the first four years of growth for peamouth caught in 1970 (□), 1971 (♦), and 1972 (+). The 1962–69 year-classes were sampled in 1970, the 1963–70 year-classes were sampled in 1971, and the 1964–71 year-classes were sampled in 1972. Data from Nishimoto (1973).

and Werner 1977) demonstrated substantial diet overlap among cohabiting fish species. However, these fish communities were highly differentiated according to habitat utilized and timing of feeding. In Lawrence Lake, co-occurring largemouth bass and bluegill sunfish utilized different sized prey (Werner et al. 1977), which

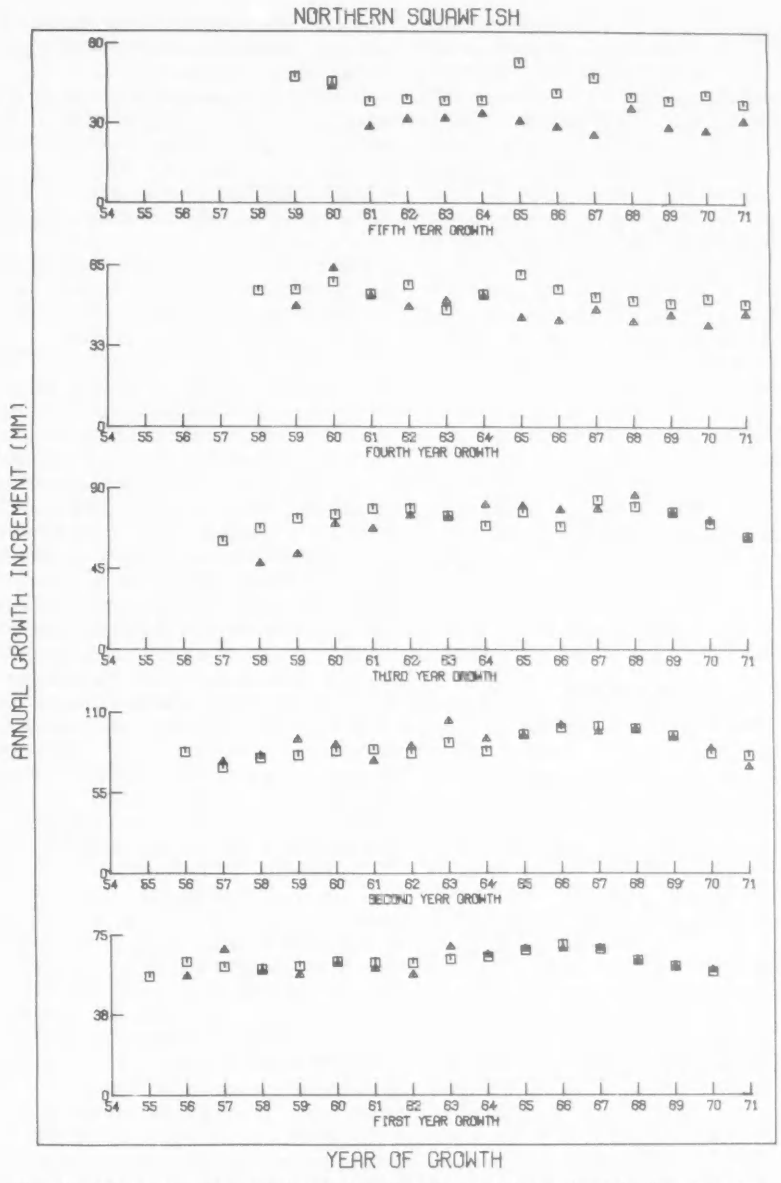

FIG. 9. Mean annual growth increments (length, mm) for each of the first 5 yr of growth (1954–72) for female (□) and male (↑) northern squawfish. Samples were collected 1971–73 for the 1955–70 year-classes. Data from Olney (1973).

reflected differences in functional morphology allowing bass to feed more efficiently on larger prey items (Werner 1977). These studies suggest that ecological segregation in fish communities is by habitat and reflects manifestation of competition.

Alternatively, it has been demonstrated that piscivorous fish predators can greatly affect the structure of fish communities. Introduction of peacock bass (*Cicla ocellaris*) in Lake Gatun, Panama, resulted in virtual extinction of the planktivorous fish population in wide areas of the lake (Zaret and Paine 1973). Introduction of largemouth bass into Lake Atitlan, Guatemala, re-

sulted in similar destruction of the native fish populations (Dorris and Summerfelt 1968, cited in Paine and Zaret 1975).

Piscivorous fish predators have an important role in determining community structure of African lakes. In African lakes having the large piscivorous predators, tigerfish (*Hydrocyon vittatus*) and Nile perch (*Lates* sp.), small fish are restricted to areas with submerged vegetation or to very shallow areas where large predators cannot maneuver (Jackson 1961). Jackson speculated that the most common reproductive behaviors of fishes in African lakes (mouth brooding, the universal reproductive strategy among African ciclids, and anadromy, in which adults migrate to riverine spawning areas) are adaptations against piscivorous predation.

Lowe-McConnell (1975), in her monograph analyzing tropical freshwater fish communities, suggested that evolution in benthic–littoral and pelagic fish communities leads to two different ends that are largely explained by the different manifestations of piscivorous predation. Benthic–littoral fish communities are characterized by a large number of cohabiting fish species with complex trophic and habitat specializations. In the benthic–littoral environment, predation restricts fish to areas of cover, effectively preventing movement between habitats and acting as an isolation mechanism (Fryer 1959). Competition for resources within this habitat further increases diversity and trophic specialization.

Pelagic environments are characterized by a uniform prey resource of small individuals. There is no cover and the only effective refuge is behavioral — that is, remaining in areas of low light intensity, schooling, and feeding briefly (Eggers 1978). Piscivorous predation in the pelagic environment does not isolate populations, rather it forces a more or less uniform behavioral response. Pelagic fish communities are characterized by few species and uniform genotype (small body size necessary to exploit zooplankton) and feeding behavior.

Northern squawfish have significant impact on juvenile sockeye salmon, the most abundant planktivore of Lake Washington. To estimate the number of juvenile sockeye eaten by squawfish, monthly values of material ingested (see footnote 6 of Table 7) were transformed into number of fish by multiplying the ration (kilograms of carbon) by the proportion of sockeye in the squawfish, then dividing by the mean body carbon content of an individual sockeye, and summing over each month of the year. This estimate applies to June 1972–May 1973 or period of lacustrine residence for the 1971 year-class of sockeye salmon, which outmigrated in 1973.

During this period, northern squawfish consumed three million juvenile sockeye salmon. The expected seasonal abundance curve, assuming northern squawfish were the agents of all sockeye mortality, seems to be consistent with observed seasonal abundance (Traynor 1973). However, sockeye were a minor (10–30%) dietary item of northern squawfish and prickly sculpin the major item (70%). If sockeye were the major dietary item, squawfish could potentially consume 22 million sockeye.

Bryant (1976) showed that in years of high sockeye abundance, sockeye experienced much higher rates of mortality during their lacustrine residence than in years of low sockeye abundance. The abundance of juvenile sockeye from the 1971 year-class was much lower than earlier year-classes that experienced much greater mortality.

These observations suggest that northern squawfish feed heavily on sockeye when sockeye are abundant and switch to prickly sculpin (the most abundant and productive species in the lake) when sockeye abundance is low. Thus, predation by northern squawfish may be a compensatory process except at very high sockeye abundance (previously not observed in the lake).

Juvenile sockeye salmon show complex feeding behavior that seems to minimize vulnerability to predation by the visual piscivore, northern squawfish, while achieving energy requirements (Eggers 1978). Longfin smelt and threespine stickleback, also planktivores, show similar feeding behavior. Northern squawfish, because of their high biomass (Table 4) and respiratory requirements, hence high ration requirement, exert significant mortality on the planktivorous fish community in Lake Washington. To avoid predators, juvenile sockeye limit the time engaged in foraging and generally occur in regions of low light intensity that are removed from regions of high zooplankton abundance. Finally, sockeye engage in schooling behavior which reduces foraging efficiency (Eggers 1976) to minimize further risk of predation. The consequences of this antipredator behavior is that planktivores exploit only a part of the total zooplankton-containing habitat in the lake.

The available information, although not as well developed as information on planktivores, implies that piscivorous predation has a substantial impact on benthic–littoral fishes in Lake Washington. Mature benthic–littoral fishes exploit prey items much larger than zooplankton, and consequently have larger body sizes than planktivores. Their large body size effectively reduces piscivorous predation. However, larval and juvenile benthic–littoral fishes are extremely vulnerable to predators. In addition to northern squawfish, yellow perch and prickly sculpin commonly feed on larval and juvenile benthic–littoral fishes (Fig. 4). Thus, this group has more potential predators than do Lake Washington planktivores.

There are three types of reproductive strategies found in the Lake Washington fish community. The eggs of sockeye salmon and longfin smelt are deposited in the Cedar River. Young-of-the-year sockeye and smelt are limnetic upon entering the lake during the spring. Prickly sculpin construct nests in littoral and profundal areas of the lake (Rickard 1978) and young-of-the-year are epibenthic. All other major species — stickleback, peamouth, squawfish, yellow perch, and suckers — are substrate spawners in littoral regions (Scott and Cross-

man 1973). Their young-of-the-year occur in a narrow band near shore in exposed littoral zones with few macrophytes. In regions with macrophyte growth, the distribution of these young-of-the-year fish is more widespread (Dykeman 1978). Cover, shallowness, and low light intensity of these habitats provide effective refugia.

Werner et al. (1977) and Hall and Werner (1977) also showed similar patterns for small fish — shiners (*Notemigonus* sp. and *Notropis* sp.), and fry and juveniles of species that are large as adults — in Lawrence Lake. DiCostanzo (1957) found year-class strength of sunfish in some Iowa lakes positively correlated with amount and distribution of macrophyte growth.

Are the abundances of benthic–littoral fish species in Lake Washington limited by resources exploited by larval and juvenile forms within these littoral and epibenthic refugia, or by the resources exploited by the less vulnerable maturing and older juvenile community? It is not clear how fry and juvenile species cohabiting in available refugia can give rise to resource partitioning among older fish not vulnerable to predation. For this to occur, the number of fish surviving the refugia must be sufficient for the resulting population, not vulnerable to predation, to deplete resources outside the refugia. In this case resource depletion would limit reproductive potential and consequently limit the input of fry to available refugia below levels that would deplete resources of the refugia. Conversely, resource limitation in the refugia would weaken the competitive interaction of adult cohabiting species.

The recruitment to the adult benthic–littoral and northern squawfish population from refugia inhabited by larvae and juveniles of these species is probably sufficient for these forms to dominate the Lake Washington fish community.

The Lake Washington planktivorous fish community depends on recruitment from the Cedar River spawning area, and on the littoral refugia in the case of stickleback. However, recruitment from these areas has not been sufficient to swamp the squawfish population. Compensatory mortality of juvenile sockeye due to northern squawfish predation has offset positive population increases in years of good survival of eggs in the Cedar River. The limnetic environment offers limited refuge from piscivore predation.

One would expect the production of planktivorous fish to be low in a system like Lake Washington where the piscivores are relatively insensitive to planktivore abundance. This is because of the age structure of the squawfish population and availability of the abundant prickly sculpin as alternative prey.

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Impact of the Introduction of Kokanee (*Oncorhynchus nerka*) and Opossum Shrimp (*Mysis relicta*) on a Subalpine Lake

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MORGAN, M. D., S. T. THRELKELD, AND C. R. GOLDMAN. 1978. Impact of the introduction of kokanee (*Oncorhynchus nerka*) and opossum shrimp (*Mysis relicta*) on a subalpine lake. J. Fish. Res. Board Can. 35: 1572–1579.

Introductions of opossum shrimp (*Mysis relicta*) and kokanee salmon (*Oncorhynchus nerka*) are common management tools for improvement of local sport fisheries. This paper summarizes published information from varied sources and presents supplemental data on the impact of these introductions on the Lake Tahoe zooplankton and fish communities. Concomitant with peak spawning runs of kokanee and the establishment and high densities of *Mysis* was the disappearance of the three pelagic cladoceran species in the lake. Population dynamics analysis of the cladoceran populations indicate that their elimination was due to increasing death rates (related to *Mysis* and kokanee predation) and decreasing birth rates (possibly related to cultural eutrophication). Changes have also been observed in the fish populations. Lake trout have altered their food habits to include large quantities of *Mysis*, but this has been done to the exclusion of other prey types. Thus, improvement in lake trout condition has been indicated only in years when *Mysis* is abundant. Recent evidence of a sustained decline in the mysid population suggests that unless lake trout shift back to more traditional food sources, their condition could deteriorate to below pre-mysid levels. Finally, mean weight and abundance of kokanee spawners have declined since the cladoceran disappearance, suggesting a negative impact on the whole population which fed heavily on cladocerans.

Key words: opossum shrimp, kokanee salmon, population dynamics, cladoceran decline, introductions, subalpine lake

MORGAN, M. D., S. T. THRELKELD, AND C. R. GOLDMAN. 1978. Impact of the introduction of kokanee (*Oncorhynchus nerka*) and opossum shrimp (*Mysis relicta*) on a subalpine lake. J. Fish. Res. Board Can. 35: 1572–1579.

Deux outils de gestion communément utilisés lorsqu'il s'agit d'améliorer les pêcheries sportives locales sont l'introduction de mysides (*Mysis relicta*) et de kokani (*Oncorhynchus nerka*). Nous résumons dans le présent article l'information publiée provenant de diverses sources et présentons des données supplémentaires sur les répercussions de ces peuplements sur les communautés zooplanctoniques et ichtyologiques du lac Tahoe. En même temps que les remontées reproductrices des kokani atteignent un sommet et que les *Mysis* s'établissent et deviennent très denses, on constate la disparition de trois espèces de cladocères pélagiques dans le lac. L'analyse de la dynamique des populations de cladocères indique que leur élimination est due à des taux de mortalité accrus (liés à la prédation par les *Mysis* et les kokani) et à une natalité réduite (possiblement liée à l'eutrophisation agricole). On observe également des changements dans les populations de poissons. Les touladis modifient leurs habitudes alimentaires pour inclure de grandes quantités de *Mysis*, mais cela s'est produit à l'exclusion des autres types de proies. On constate donc une amélioration dans la condition des touladis seulement dans les années où les *Mysis* sont très abondants. La preuve récente d'un déclin graduel de la population de mysides donne à croire que la condition des touladis pourrait se détériorer au point de tomber à des niveaux inférieurs à ceux d'avant-mysides, à moins que ces touladis ne retournent à des sources de nourriture plus traditionnelles. Finalement, le poids moyen et l'abondance des kokani reproducteurs on décliné depuis la disparition des cladocères, ce qui suggère une répercussion négative sur la population entière qui se nourrissait abondamment de cladocères.

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MANY dramatic changes have occurred in the limnetic features of Lake Tahoe since the development of its basin. Perhaps the earliest major change was the collapse of the native cutthroat fishery in the 1930s. In good years, up to 34 019 kg of fish were harvested (Juday 1907). This fishery was replaced by one for the lake trout (*Salvelinus namaycush*), a species first introduced into the lake in 1889 (Miller and Alcorn 1945). The lake trout fishery never equaled pre-1930 cutthroat fishery yields (Weidlein et al. 1965), and discontent by basin fishermen over poor fishing conditions resulted in a number of management decisions that have had marked effects on the biology of the lake. In particular, three species were introduced into the lake between 1944 and 1965 in an attempt to provide forage for lake trout or to provide additional types of fisheries (cisco, Frantz and Cordone 1965; kokanee salmon, Cordone et al. 1971; opossum shrimp, Linn and Frantz 1965 and Hanson 1966). The purpose of this paper is to summarize available information on the range of direct and indirect effects that have resulted from the introduction of two of these species, the kokanee salmon (*Oncorhynchus nerka*) and the opossum shrimp (*Mysis relicta*).

Establishment and Dynamics of Introduced Species

Mysis relicta

Mysis relicta Lovén, a freshwater representative of the predominately marine order Mysidacea, naturally inhabits northern, deep, coldwater lakes in areas of extensive Pleistocene glaciation (Holmquist 1959). Its large size (up to 3.0 cm) and benthic and planktonic habits make it a desirable food item for a wide variety of commercial and sport fish. *Mysis* has been shown to constitute a significant portion of the diets of alewives (*Alosa pseudoharengus*), bloater (*Coregonus hoyi*), rainbow smelt (*Osmerus mordax*), and burbot (*Lota lota*) (Bajkov 1930; Schneberger 1936; Van Oosten and Deason 1937; Stone 1944; and Larkin 1948). Of primary interest here, however, is the importance of *Mysis* in the diets of lake trout, which are the primary sport fish of Lake Tahoe. Several studies indicate that *Mysis* is an important dietary component of juvenile lake trout in other lakes (e.g. Hacker 1956; Dryer et al. 1965). However, before the introduction of *Mysis* in Lake Tahoe, no organism naturally occurred that occupied a similar role in the diets of small lake trout. Young lake trout fed primarily on small pelagic crustaceans (Frantz and Cordone 1970) and showed poor growth compared with other lakes where more appropriate forage was available (Hanson and Cordone 1967). It was believed that establishment of *Mysis relicta* in Lake Tahoe would substantially increase the growth and survival of these trout (Linn and Frantz 1965). Toward this end, from 1963 to 1965, the California and Nevada Departments of Fish and Game introduced approximately 333 000 mysids collected from Waterton Lake, Alberta, and Green Lake, Wisconsin, into Lake Tahoe (Linn and Frantz 1965; Hanson 1966).

The success of this introduction was first suggested in 1969 by the first appearance of mysids in daytime benthic trawls equipped with a 1-m² mouth, 500-μm plankton net and stomachs from angler-caught lake trout (Fig. 1). From

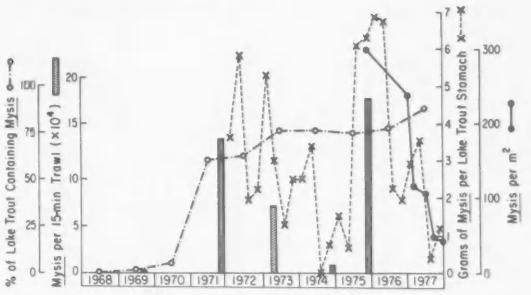

FIG. 1. Four estimates of relative *Mysis* density in Lake Tahoe: (1) Frequency of 38–51-cm lake trout caught by basin fishermen containing *Mysis* (annual averages; data from Frantz 1970–78); (2) *Mysis* collected per 15-min daytime benthic trawl (Richards et al. 1975, Wickwire unpublished data); (3) grams of *Mysis* per lake trout stomach containing *Mysis* (seasonal averages: data from Frantz 1973–78); (4) mean number of *Mysis* per square metre as estimated from nighttime vertical net tows (Goldman et al. 1979).

1969 to 1971, dramatic increases in both of these indications of *Mysis* density were noted and it appeared that by 1971 *Mysis relicta* was well established in Lake Tahoe.

Although quantitative estimates obtained with nighttime vertical net tows with a ¾ m, 500-μm mesh plankton net are available only since late 1975, relative measures of *Mysis* density have revealed considerable fluctuation since their establishment in 1971. In particular, both benthic trawls and the weight of *Mysis* found in lake trout stomachs declined from 1972 to early 1975. Also, from late 1975 to the present, population size has declined steadily as revealed by both lake trout stomach contents and nighttime vertical net tows (Fig. 1).

We obtained detailed information on the lakewide distribution and abundance of *Mysis* from nighttime vertical net tows taken on four synoptic surveys in 1977. Stations were concentrated near the shore where most of the variability in mysid numbers occurred. In all surveys, the four deep water stations (>400 m) sampled on the same date yielded remarkably consistent values (average C.V. 27.2%). Contour maps that resulted from two of these cruises are presented in Fig. 2. Clearly *Mysis* has become established throughout the lake, although the recent decline in mysid abundance is also very much apparent. Although abundance varies considerably from one date and station to another, densities in shallow water (<50 m) are always considerably lower than those found in deeper water. Another pattern revealed by the synoptic surveys is the pronounced effect of temperature on the horizontal distribution of *Mysis*. In February, mysids were found in appreciable numbers at 11 of the 12 stations at a temperature of about 6.2°C in water <20 m deep. In contrast, the August survey failed to find mysids at any of these stations, although 27 m^{-2} were found at one 26-m station. Beeton (1960) and Teraguchi (1969) have shown that a well-defined metalimnion will set an upper limit on mysid vertical migration. In August this layer extended from about 23 to 35 m in Lake Tahoe. Thus, the horizontal distribution of *Mysis* also seems limited by temperature; as summer stratification proceeds, mysids must migrate to deeper, cooler waters.

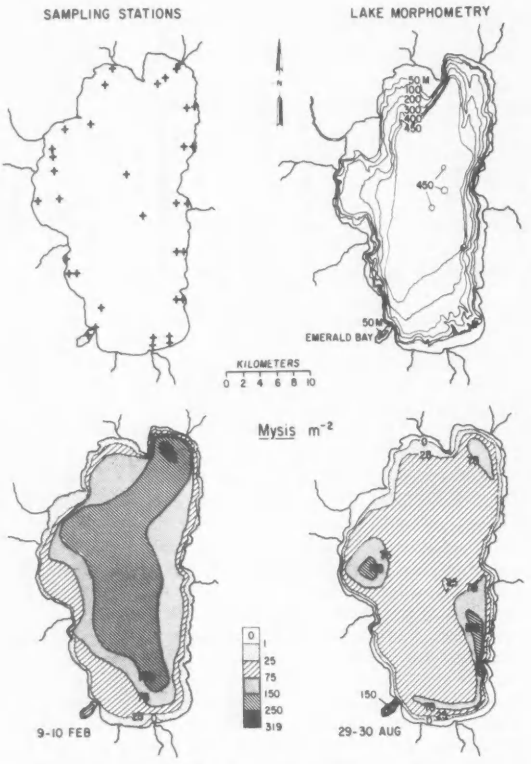

FIG. 2. Lakewide distribution and abundance of *Mysis relicta* in Lake Tahoe. Upper maps show the location of sampling stations and lake morphometry. Lower maps indicate isopleths of *Mysis* density in February and August 1977.

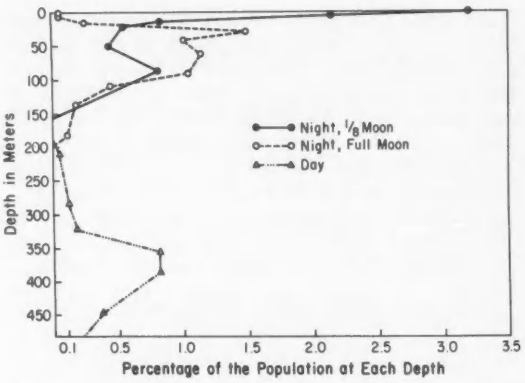

FIG. 3. Vertical distribution of *Mysis* in Lake Tahoe during daylight and according to the phase of the moon (J. T. Rybock unpublished data). Absolute *Mysis* densities have been scaled to the percentage of the total population found at each depth so that the areas under the curves are constant for the three sampling dates shown.

The vertical distribution of *Mysis* as determined by horizontal tows with an opening closing tucker trawl (500-μm mesh) equipped with a time-depth recorder is also influenced by light. During the day *Mysis* remains pelagic in waters deeper than 200 m, while in shallower areas the animals are benthic. At night, light is also important, with the vertical distribution varying with the phase of the moon (J. T. Rybock, Tahoe Research Group, P.O. Box 633, Tahoe City, Calif., unpublished data). During full moon, mysids are most concentrated from 25 to 100 m, but with little moonlight the animals are generally concentrated near the surface (Fig. 3).

Lake Tahoe is a deep, steep-sided lake (mean depth = 313 m), so that more than 70% of the lake surface lies over water deeper than 200 m (Abrahamsson and Goldman 1970). Consequently, the majority of the mysid population in Lake Tahoe can be viewed as pelagic, a fact that may have considerable bearing in their vulnerability to benthic predators such as lake trout.

Oncorhynchus nerka

Kokanee salmon were first introduced into Lake Tahoe in 1944 when fry held at the Tahoe State Hatchery at Lake Forest were released accidentally. Since that time, the Fish and Game departments of Nevada and California have attempted to establish a self-sustaining fishery for this species in the lake. In addition to providing forage for subadult and adult lake trout, it was hoped that a kokanee fishery would increase the total sports fishery yield from the lake by feeding on previously underutilized crustacean zooplankton (Cordone et al. 1971). The kokanee stocking records are given in Table 1.

TABLE 1. Time and number of kokanee plantings into Lake Tahoe (Frantz personal communication).

Kokanee stocking records	
Year	Number
1950	500 300
1951	392 064
1952	623 585
1953	176 810
1954	308 565
1955	78 720
1965	339 000
1967	3 138 648
1968	1 562 900
1969	1 633 005
1977	13 320

In Lake Tahoe, kokanee generally spawn in the fall at 3 yr old, although some 2 and 4 yr olds are also present (Cordone et al. 1971; R. Wickwire, California Department of Fish and Game, Tahoe City, Calif., personal communication). Spawning is concentrated in Taylor Creek, the outflow of Fallen Leaf Lake into Lake Tahoe. Other streams have never had significant runs. Information on the establishment and fate of kokanee in Lake Tahoe comes primarily from direct counts of the size of the Taylor Creek spawning runs. Low spawning runs were observed before

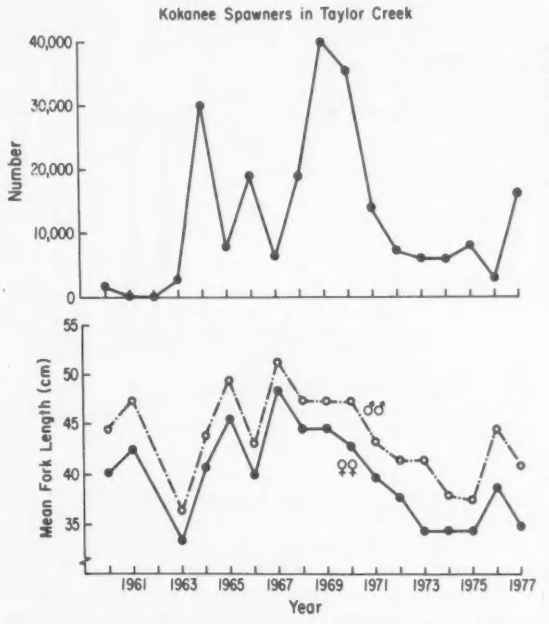

FIG. 4. Annual number and mean body length of kokanee spawners in Taylor Creek (Frantz 1970–78; Wickwire unpublished data).

1964, when the number of spawning kokanee increased (Fig. 4). Following several years of erratic spawning runs, peak runs were observed in 1969 and 1970, when conditions in Taylor Creek became so crowded that many kokanee were found spawning in shallow areas along the shore of the lake. This is the only time significant shore spawning has been observed (Wickwire personal communication). Following the peak runs of 1969 and 1970 the number of kokanee spawners steadily decreased until 1977.

The mean body size of spawning kokanee has also exhibited considerable fluctuation since 1960. Although quite variable until 1966, a peak in mean body size was observed in 1967. Since then, body size of spawning kokanee has generally decreased (Fig. 4).

Impact of Introductions

The research efforts of the Tahoe Research Group (University of California, Davis) and the Fish and Game departments of the states of Nevada and California have revealed dramatic changes in the zooplankton and fish of Lake Tahoe following these species introductions. As will be discussed later, the changes that have occurred in the fish appear at least partially related to changes that have occurred in the zooplankton. As a result, we begin by discussing the dynamics of the zooplankton populations as influenced by these species introductions.

Zooplankton Population Dynamics

As reported by Goldman (1974), Richards et al.

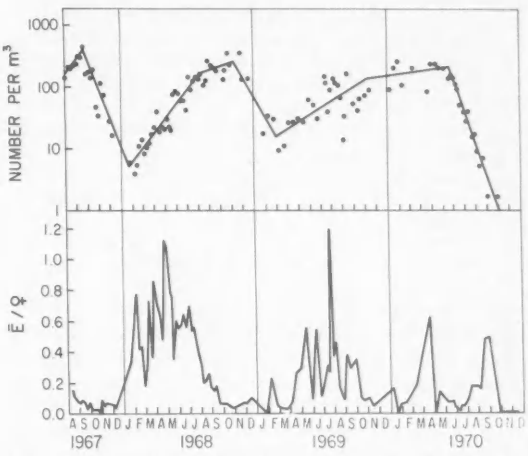

FIG. 5. Logarithmic plot of mean density and egg ratio ($\bar{E}$) of *Daphnia* in Lake Tahoe, 1967–70. Least-squares regression lines have been fitted to the density data for periods of sustained increase or decrease. After Goldman et al. (1979).

(1975), and Goldman et al. (1979), concomitant with the establishment of *Mysis relicta* and peak spawning runs of kokanee were the decline and disappearance of the cladoceran species *Daphnia pulicaria*, *D. rosea*, and *Bosmina longirostris* from the plankton. Before this, cladocerans were significant members of the zooplankton, both in terms of biomass and numbers.

Goldman et al. (1979) have reviewed the dynamics of *Bosmina* and *Daphnia* based on an extensive data base of vertical net tows at least every 2 wk before, during, and after the decline periods in 1970 and 1971. Population growth rates (r) of *Daphnia* were calculated from least-squares regressions of abundance over periods of sustained increase or decrease (Fig. 5). Estimated birth rates ($\bar{b}$) were determined from *Daphnia* female/egg ratios and published information on temperature-specific egg development times. *Daphnia* death rates ($\bar{d}$) were then obtained by difference ($\bar{d} = \bar{b}$-r).

Goldman et al. (1979) attributed the final decline of *Daphnia* in 1970 to a combination of increased population death rates and decreased birth rates as compared with similar periods in earlier years (Table 2). The decline in birth rates may have been due to annual variation in the timing of primary production and the quantity of phytoplankton biomass available as food in the water column. The increase in death rates was probably due to increased predation pressure from the increased densities of *Mysis* and kokanee. Goldman et al. further suggested that the decline of *Bosmina* and *Daphnia* probably resulted from slightly different combinations of similar factors, with the two cladocerans (which differ considerably in size) having different susceptibilities to kokanee and *Mysis* predation. This view is supported by the different timing of the decline of

TABLE 2. Average birth ($\bar{b}$) and death rates ($\bar{d}$) of *Daphnia* in Lake Tahoe during the period of final decline in 1970 and for similar periods in 1968 and 1969. See Goldman et al. (1979) for details of calculations and raw values.

June–Dec.	$\bar{b}$	$\bar{d}$
1968	0.015	0.019
1969	0.013	0.006
1970	0.007	0.043

these two cladocerans (Fig. 5; Fig. 6), as well as published information that suggests size-related vulnerability to vertebrate and invertebrate predators (see review by Hall et al. 1976).

In addition to insights gained directly from analyses of population dynamics before and during the decline of *Bosmina* and *Daphnia*, Goldman et al. (1979) have been able to evaluate some of their ideas by the subsequent behavior of zooplankton populations in Lake Tahoe. For example, the idea that *Bosmina* is particularly vulnerable to predation by *Mysis* was tested in late 1974 and early 1975 when *Mysis* densities apparently declined (Fig. 1). During this period *Bosmina* made a temporary resurgence (Fig. 6), consistent with the idea that *Mysis* predation is of importance to these cladocerans. However, it was also during this time that another predator of *Bosmina*, *Epischura nevadensis* (see Kerfoot 1975), briefly declined (Fig. 6), making specific assignment of the cause of the *Bosmina* reappearance uncertain. We currently have conditions that may help us to evaluate the effects of *Mysis* and *Epischura* predation on *Bosmina*, as *Mysis* densities are again on the decline, although those of *Epischura* are not (Goldman et al. unpublished data). The lack of reappearance by *Daphnia* with the 1974 and most recent *Mysis* declines and decreases in kokanee spawners suggests that other causes are contributory to their continued absence, perhaps changes in primary productivity and phytoplankton biomass.

CHANGES IN KOKANEE AND LAKE TROUT

Changes in the fish of Lake Tahoe appear most closely related to changes in the zooplankton. Before their elimination in 1970, cladocera (primarily *Daphnia*) were the primary food source for kokanee in the limnetic zone (Cordone et al. 1971). Since the elimination of cladocera from the zooplankton, kokanee have included more copepods in their diet, and there has been some tendency to include *Mysis*, although only larger kokanee appear to use this food source (Table 3). That mysids and copepods do not adequately substitute for the now absent cladocerans is demonstrable in two ways.

As pointed out earlier, kokanee spawning runs and mean body size of spawners have declined since the elimination of cladocerans. The cladoceran decline also

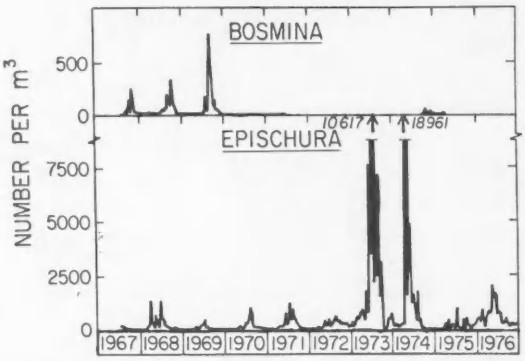

FIG. 6. Mean density of *Bosmina* and *Epischura* expressed as individuals per cubic metre from 1967 to 1976. After Goldman et al. (1979).

seems to have affected the kokanee stock–recruitment relationship. Although detailed information on kokanee life history in Lake Tahoe is unavailable and so a strict stock–recruitment relationship cannot be worked out, some idea of this relationship can be obtained by comparing spawning run size with the spawning run size 3 yr later (the time normally required for juveniles to reach reproductive age). This relationship appears highly density dependent. In years of low spawning runs, recruitment was high, and lower in years of high spawning runs (T. C. Frantz, Nevada Department of Fish and Game, P.O. Box 472, Smith, Nev., unpublished data). On the basis of the years 1963–69 (those years when young-of-the-year kokanee could feed on cladocerans), approximately 15 000 kokanee could be expected to exactly replace themselves (Fig. 7). However, since the decline of cladocerans, the kokanee population that could be expected to sustain itself measures only about 7000 fish.

The effect of kokanee stocking could invalidate this type of analysis if the stocking program were successful

TABLE 3. Food habits of kokanee salmon as revealed by the percentage of kokanee found to contain copepods, cladocerans, and mysids. Data from Frantz 1970–77 and is based on angler catches throughout the year.

Year	*n*	Kokanee size-class (*cm*)	Prey category		
			Copepods	Cladocerans	Mysids
1963–64	74	25–33	26	89	0
	41	38–51	14.6	100	0
1972	41	25–38	70.7	4.9	9.8
	44	38–51	39	17.1	24.4
1974	52	25–38	78.8	5.8	1.9
1975	86	25–38	98.7	0	12.8
	2	38–51	0	0	100
1976	9	25–38	88.9	0	0
	12	38–51	33.3	0	50

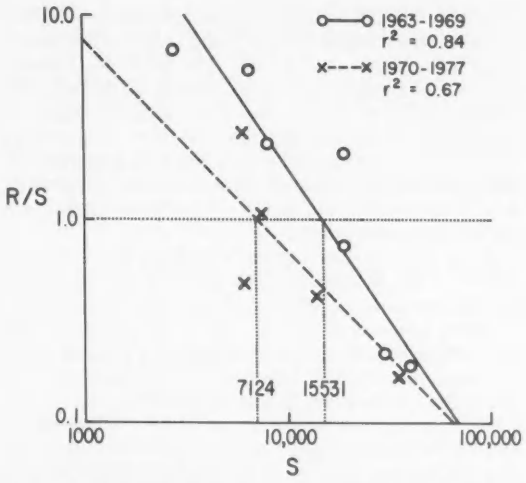

FIG. 7. Relationship between the recruitment of kokanee to spawning age (assumed to be 3 yr) per spawning kokanee (R/S) and the size of the spawning population (S) for the years 1963–69 and 1970–77. Equilibrium, or self-sustaining, populations of kokanee for the two time periods are estimated where least-squares regressions predict values of R/S = 1.0, and are projected to the abscissa.

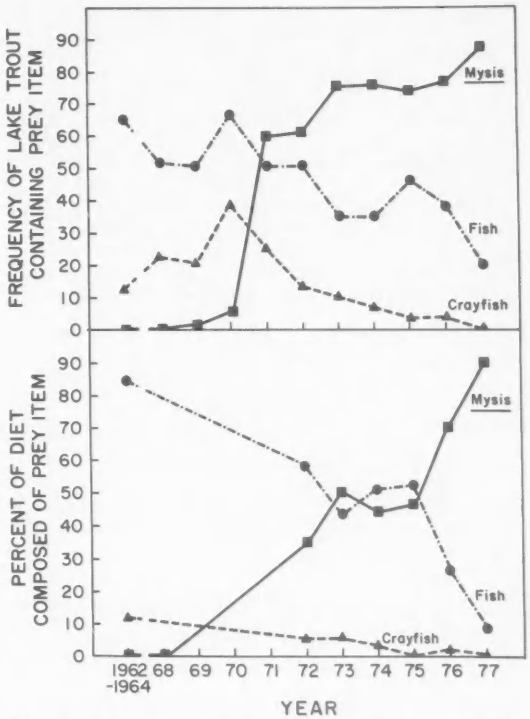

FIG. 8. Frequency of lake trout stomachs containing *Mysis*, fish, and crayfish (top panel) and the average percentage, by weight, of each of these items in the stomachs (lower panel) from 1962 to 1977. Note the break in the time scale between 1964 and 1968.

in increasing the kokanee population. However, from 1964 to 77, during the years of heaviest stocking (Table 1), no relationship could be found between the number of fish stocked and the spawning size 3 yr later ($r = 0.35$, $P > 0.05$). This suggests that stocking had little impact on the overall lake population.

These findings indicate that the prime food source for kokanee before 1970, *Daphnia*, was a necessary ingredient to pre-1970 growth and recruitment relations exhibited by kokanee. Thus, through their contribution to the elimination of *Daphnia*, both kokanee and *Mysis* have adversely affected the future of kokanee in Lake Tahoe. It is questionable whether introduction of kokanee alone would have resulted in a stable *Daphnia*–kokanee relationship since we are uncertain about the relative importance of *Mysis* and kokanee to the cladoceran decline.

The response of lake trout to these introductions has been mixed. Lake trout have substantially shifted their feeding from crayfish and benthic and pelagic fish to *Mysis*, since their establishment in the lake around 1970. This is indicated both by the contribution of *Mysis* to lake trout stomach contents and the frequency of lake trout that consume *Mysis* (Fig. 8). However, despite the hopes of fisheries managers, the increased utilization of *Mysis* has not led to any significant overall improvement in lake trout condition (Frantz 1970–78).

Over the years when *Mysis* has been available, the lake trout length–weight relationship has fluctuated considerably. A large part of this variability is attributable to the amount of *Mysis* lake trout have consumed (for 1972–77, $r = 0.842$, $P < 0.05$). Although there has not been any overall improvement in the lake trout length–weight relationship, there does seem to have been a positive response in those years when *Mysis* was particularly abundant in trout stomachs (e.g. 1973 and 1976) as compared with 1970 when *Mysis* was rarely consumed (Frantz 1971, 1974, 1977; Fig. 9). Thus, it appears that *Mysis* has been successfully added to the lake trout diet, but only at the expense of other food sources, and that the shift to *Mysis* has been beneficial only when *Mysis* are abundant. Should the present decline in mysid abundance continue and the lake trout not revert to more traditional food sources, lake trout condition could decline even below the pre-mysid levels.

Discussion

The introductions of kokanee and *Mysis* into Lake Tahoe appear to have contributed to dramatic changes in zooplankton. In addition, the kokanee introduction has not led to a significant fishery for this species. The only positive effect of the introductions has been an

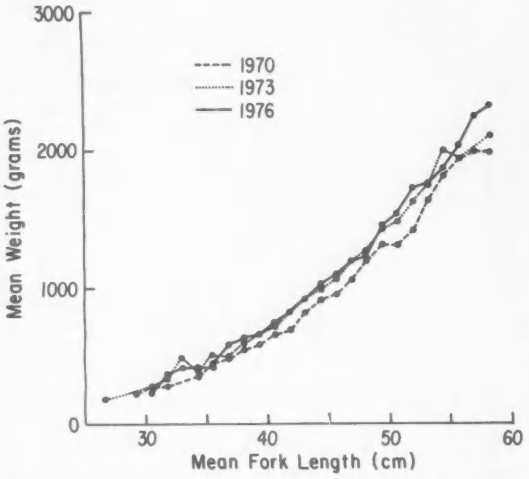

FIG. 9. Length–weight relationships for lake trout caught by basin fishermen in 1970, 1973, and 1976 (data from Frantz 1971, 1974, 1977).

apparent stimulation of lake trout growth in some years when *Mysis* is abundant, although even this effect has not been sustained and may be reversing with the current decline of *Mysis*.

Mysis and kokanee have been introduced into a large number of freshwater lakes, and the results of the Lake Tahoe experiment seem at odds with results obtained in these other systems (Gosho 1975). The results of Northcote (1972a, b, 1973) on kokanee growth in Kootenay Lake, British Columbia, before and after the introduction of *Mysis* and a period of cultural eutrophication, provide an interesting contrast to the Lake Tahoe results. Particularly noteworthy has been a major increase in growth rate, modal length, and length–weight relationships among kokanee in the west arm of Kootenay Lake, where especially heavy use of *Mysis* by these fish occurs. Juvenile kokanee appear to rely heavily on copepods, while *Mysis* are consumed by subadults and adults.

Two significant differences between Kootenay Lake and Lake Tahoe may account for these results and pertain to the availability of mysids to the kokanee and suitable prey resources for juvenile kokanee. First, the density of copepods available for consumption by juvenile kokanee in the west arm of Kootenay Lake is as high as an order of magnitude greater than in Lake Tahoe (Zyblut 1970; Goldman unpublished data). Undoubtedly, the greater primary productivity of Kootenay Lake accounts for these higher standing crops of zooplankton; it may be that this more plentiful food resource permits kokanee growth to a size where *Mysis* are readily and efficiently consumed. Second, the shallow nature of the west arm (mean depth = 13 m) probably results in a greater availability of *Mysis* to the kokanee. In contrast, the daytime distribution of *Mysis* in Lake Tahoe below 200 m (Fig. 3) makes them essentially unavailable to kokanee. The fact that kokanee growth in the south and north arms of Kootenay Lake (mean depth = 102 m) has not been increased as dramatically by the presence of *Mysis* (Northcote 1973) lends support to the idea that mysid availability, which is probably most influenced by lake bathymetry, is critical to the stimulation of kokanee growth observed in the west arm.

From these considerations it appears that lake productivity and morphometry are critical to the success of introductions of *Mysis* and kokanee. In shallower or more productive systems, these introductions have not resulted in the complete elimination of cladoceran populations, although some species shifts have been noted (see review by Gosho 1975). The inability of Lake Tahoe's cladocerans to withstand the additional mortality caused by these predators appears due to the system's low productivity and lack of population control on the introduced predators. Because of Lake Tahoe's great depth, it is doubtful that either kokanee or lake trout could have effectively controlled *Mysis* population growth and establishment around 1970 when the impact of *Mysis* on cladocerans was maximal. In addition, because kokanee and lake trout do not overlap greatly in their depth distribution, kokanee were probably also an uncontrolled predator on the lake's cladocerans. Thus the very low productivity and great vertical expanse of the Lake Tahoe environment resulted in dramatic changes in the food web, rather than a successful addition of new species without elimination of preexisting ones. These replacements have had an adverse effect on the growth and recruitment of kokanee, and it is unclear what will be the ultimate fate of *Mysis*, kokanee, and lake trout in Lake Tahoe. We are not optimistic that these introductions will have a lasting benefit for basin fishermen.

Acknowledgments

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Enhancement of Sockeye Salmon (*Oncorhynchus nerka*) by Lake Fertilization in Great Central Lake: Summary Report

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Great Central Lake was treated with ca. 100 t of commercial grade fertilizer (ammonium nitrate and ammonium phosphate) annually from 1970 through 1973. Limnological parameters and sockeye salmon (*Oncorhynchus nerka*) juveniles and adults were monitored from 1969 through 1976 to test the hypothesis that increasing the supply of inorganic nutrients in an ultraoligotrophic lake would increase production at succeeding trophic levels. Rates of change and linkages between different elements of the food chain leading to juvenile sockeye salmon were identified. During fertilized years mean summer primary production increased fivefold, zooplankton standing stock increased 9 times, the percentage survival from estimated potential egg deposition to juvenile sockeye increased 2.6 times, while mean stock size of adult sockeye increased from $<50\,000$ to $>360\,000$. Adult sockeye returning to an adjacent untreated lake also increased in abundance. The data for the 8-yr period support the initial hypothesis, but the dominant processes affecting production and interrelationships between different trophic levels in different years remain masked.

Key words: food chain, limnology, sockeye salmon, primary production, zooplankton, eutrophication, lake fertilization, enhancement

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De 1970 à 1973 inclusivement, on a traité annuellement le Grand lac Central avec approximativement 100 tonnes d'engrais commercial (nitrate d'ammonium et phosphate d'ammonium). On a suivi, de 1969 à 1976 inclusivement, les paramètres limnologiques ainsi que les jeunes et les adultes de saumon nerka en vue de vérifier l'hypothèse qu'une augmentation d'apports d'éléments nutritifs inorganiques dans un lac ultra-oligotrophe augmenterait la production aux paliers trophiques suivants. Les taux de changement et les relations entre les différents éléments de la chaîne alimentaire conduisant aux jeunes saumons nerka ont été identifiés. Dans les années où il y eut fertilisation, la production primaire estivale moyenne augmenta de 5 fois, la biomasse de zooplancton de 9 fois, le pourcentage de survie d'une ponte potentielle estimée au stade juvénile augmenta de 2.6 fois, alors que la taille moyenne du stock de saumons nerka adultes passa de $<50\,000$ à $>360\,000$. Les saumons nerka adultes retournant à un lac avoisinant non traité augmentèrent également d'abondance. Les données couvrant une période de 8 ans corroborent l'hypothèse initiale, mais les processus dominants affectant le production et les relations entre différents paliers trophiques d'une année à l'autre demeurent masqués.

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BETWEEN 1970 and 1973 inorganic nutrients were added to Great Central Lake in an attempt to increase juvenile sockeye salmon (*Oncorhynchus nerka*) production. Information was collected before, during, and after fertilization on primary production, abundance, and composition of zooplankton, food, growth, and survival of juvenile sockeye in the lake and returns of adult salmon to the lake. The purpose of this report is to summarize these data for the period 1969 through 1976.

It was earlier proposed (Foerster 1968) that a lake system with low nutrient concentrations could be stimulated by fertilization to increase the rate of primary

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production and hence the supply of food to herbivorous zooplankton which would provide more food for juvenile sockeye during their lake residence. It was hypothesized that increased food would lead in turn to increased growth and survival of juvenile sockeye, and hence to enhanced returns of adult salmon. In essence, the major twin assumptions were that Lindëman's trophic dynamic model applies: 1) the formation and flow of energy from one trophic level to the next is measurable; 2) the yield of sockeye smolts is limited by food supply (secondary production).

Study Site

Great Central Lake (Fig. 1) was chosen as an experimental site because of its low nutrient content and loading, low rate of primary production, small standing stock of zooplankton, moderate size, relatively great depth, preponderance of steep rocky shores with minimal attached vegetation, thermal stratification in summer, and a fish fauna dominated by underyearling sockeye salmon. Its proximity to the research facilities at Nanaimo and the availability of a field camp and other facilities at nearby Robertson Creek provided logistic advantages.

The ultraoligotrophic characteristics of Great Central Lake have been reported in detail earlier (Parsons et al. 1970, 1972; Barraclough and Robinson 1972; LeBrasseur and Kennedy 1972; McAllister et al. 1972; Barraclough et al. 1974; Takahashi and Nash 1973; Manzer 1976b). The lake is about 34 km long, 1.5 km in mean width, has a mean depth of about 200 m and a maximum observed depth of 273 m. Its waters are thermally stratified between April and November, with a mean epilimnion depth of about 10 m, and the bottom of the thermocline at about 20 m. Epilimnial temperature may exceed 20°C during July, August, and September. Temperature at 25 m fluctuates narrowly about 6.5°C during summer. The water is clear, with mean Secchi disk depth reading exceeding 12 m. All or part of the lake may freeze over during the winter for periods of 1–2 mo.

Circulation in the upper 10 m is dominated by the wind, but affected by temperature distribution and plunging inflow of cold streams at the head of the lake, particularly during spring and fall. Water retention in the epilimnion between April and November is estimated to range from 15–55 d, averaging about 40 in summer.

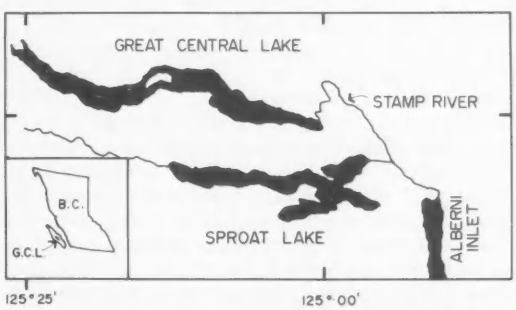

FIG. 1. Great Central Lake and adjacent Sproat Lake. The unshaded area on Great Central Lake represents the area receiving controlled additions of inorganic nutrients.

Methods

General

Methods used in this study have been described in a series of reports (Appendix 1) and will be presented only briefly here as they pertain to interpretation of results. Data were collected on a wide variety of physical, chemical, and biological features of the lake before, during, and after nutrient additions (Appendix 1). During fertilization (1970–73) observations were made at least once a week. During fall, winter, early spring, and after cessation of enrichment, the observations were at biweekly or sometimes monthly intervals. Abundance and distribution of juvenile sockeye were determined by echo sounding and trawling at approximately 3-wk intervals between April and November. Sockeye smolts and adults were sampled during their migration for age and size composition. In addition, information on cutthroat trout (*Salmo clarkii*), coho salmon (*O. kisutch*), and stickleback (*Gasterosteus aculeatus*) has been reported for Great Central Lake by Narver (1975), Mason (1974), and Manzer (1976a), respectively.

In general, all the latter studies reflect simple community structures and relationships. The trout range throughout the lake and while primarily feeding on insects they do prey on sockeye eggs and juveniles. The coho salmon occupy the littoral area and feed exclusively on insects. Stickleback were found mainly in the littoral area where they feed on zooplankton and, to a lesser extent, insects. In the above studies there was no evidence of any significant interaction between any of the fish species and juvenile sockeye. By the end of the experiment in 1976 there was some circumstantial evidence that the trout population had increased.

Fertilization

Nutrient additions to Great Central Lake were designed to maintain epilimnial concentrations at the levels observed following overturn (2 μg-atoms NO_3-N and 0.03 μg-atoms P/L). We hoped to achieve a sustained increase in the rates of primary and secondary production, while avoiding nuisance blooms of algae.

Ammonium phosphate and ammonium nitrate to be added to the lake were dissolved separately and combined in proportions giving an atomic ratio of nitrogen to phosphorous of 10:1. The total annual loading of elemental nitrogen and phosphorous was 33 t. Calculated on the basis of lake surface area, the phosphorous loading was approximately 0.05 g/m^{-2} which is equivalent to about 22% of the permissible loading (Vollenweider 1976). The dissolved nutrient mixture was usually spread in 5-t aliquots once weekly over a 20-wk season at the lake surface in the wake of a moving boat over a 5–10-km portion of the lake. The annual supply of nutrients to a 30-m water column in the lake represented a 100% increase in the inorganic nitrogen budget and a 450% increase in the phosphate supply. The nutrient additions were maintained between May and October of 1970–73 inclusive. The fertilization area was located away from the mouth of the lake to minimize the chance of any nutrients being flushed out (Parsons et al. 1970, 1972). For a 6-wk period in 1971 when water temperatures were maximal, fertilizer was injected at a depth of 10 m in an attempt to increase food production nearer to depths at which fish were feeding.

Standard methods for determining primary production,

chlorophyll *a* and nutrient analyses were employed (Strickland and Parsons 1968). Phytoplankton species and cell counts were made using an inverted microscope. Sampling frequency, depths, and locations are reported in manuscript reports listed in Appendix 1.

Zooplankton

Methods employed in studies of zooplankton have been described by LeBrasseur and Kennedy (1972). In this report, zooplankton biomass estimated from species counts in samples collected by 50-m vertical net hauls at two stations one inside the treated portion of the lake, the other outside are discussed. During the growth season in years of fertilization sampling was every 4 d. At other periods of the year, and in nontreatment years, sampling was biweekly. Zooplankton counts were converted to wet weight per square metre ($g \cdot m^{-2}$) from species length–weight regressions. The data are recorded in annual data reports (Appendix 1).

Juvenile Salmon

Methods of sampling sockeye salmon juveniles, presmolts, and smolts; description of fishing gear; and the laboratory methods for measuring size and weight, determining age composition, and conducting food analyses are presented in more detail in Barraclough and Robinson (1972) and in various data reports listed in Appendix 1.

To assess abundance and monitor horizontal and vertical distribution of young sockeye, echo-sounder surveys with a high frequency transducer (200 kHz) were made over a standard grid running along and across the lake. These surveys were made biweekly throughout the late spring and summer, then monthly throughout the fall and winter, ice cover permitting.

Juvenile sockeye were sampled at six standard stations in the lake by fishing with a 3-m × 6-m midwater trawl. Sampling commenced about 1 h after sunset (civil twilight) at which time the young fish had completed their upward vertical migration and were most accessible to the trawl net.

Further echo-sounder estimates of abundance of juveniles were made at these six stations at the time of fishing to assess trawl efficiency under measured levels of light intensity.

The diel pattern of feeding of young sockeye was obtained from a series of samples taken over 24-h periods, during four years.

Samples of smolts were obtained downstream from the lake outlet on a small bypass creek joining the Stamp River which carries some of the discharge from Great Central Lake (Fig. 1).

Age of individual sockeye was determined from scale readings.

Adult Salmon

Catch and escapement data were provided by the Fisheries and Marine Service, Port Alberni, B.C. The total run in a given year to both Great Central Lake and Sproat Lake was estimated by prorating the commercial catch by the estimated escapement to each lake, and summing the respective catch and escapement figures. Passage of the two stocks through the fishery is believed to be similar in time (Manzer, 1972), so it is assumed that fishing rate on each stock is concurrent and equal.

Estimates of sockeye salmon returns (catch plus escapement) to Great Central and adjacent Sproat Lake for the period 1958–75 inclusive are reported (Manzer 1976b). The runs produced by spawning escapements prior to 1969 represent returns from pretreatment brood years; those produced by escapements from 1969 to 1972 represent treated brood years. For practical purposes we consider that the returns of progeny from treated brood years will be completed in 1977.

The effect of fertilization on the sockeye runs was evaluated by three methods:

1. Comparison of average run size before treatment (15 yr, 1958-1972) with that during treatment (4 yr, 1973-1976) for both Great Central Lake and for untreated Sproat Lake nearby.
2. Comparison of estimated total run to reproductive success of Great Central and Sproat lakes.
3. Comparison of reproductive success of treated and untreated escapements to Great Central Lake since 1956.

Age composition of the commercial catch and/or escapement was used to assign returning adults to their appropriate brood year. Catch and escapement to each system were weighted for seasonal variation in age composition, and for bias introduced by gillnet selectivity for larger, older fish. The method for calculating reproductive success for a given brood year is described by Manzer (1972).

Results

Primary Production

Annual primary production in the upper 30 m in fertilized years (1970–73 inclusive) averaged 1.8 times that in post-treatment years (1974, 1975, and 1976) (Table 1a). For the same depth range, chlorophyll *a* was higher in the fertilized years, but to a lesser degree than was primary production. Similarly, the ratio, primary production/chlorophyll *a* averaged higher during years of fertilization. The higher chlorophyll *a* values in the 30-m column reflect concentrations of *Rhizoselenia* sp. at the bottom of the thermocline, ca. 25 m. Annual primary production in 1976, a year of no fertilization, was relatively high and exceeded that in 1973, a fertilized year. In 1976 winter production was high while summer production was low.

Primary production in the fertilized years during June, July, and August, the months of peak production, was greater than that in the postfertilization years, 1974–76 (Table 1B). Production in the upper 10 m, during fertilization, was over 5 times and in the upper 30 m was over 2 times the mean production after fertilization was stopped. Chlorophyll *a* and the ratio production/chlorophyll *a* were greater during fertilization, particularly in the upper 10 m. Ratios of primary production to chlorophyll *a* in the upper 10 m reflect nutrient additions, but not concentration. Very rapid uptake of nutrients by phytoplankton must be postulated. The massive but transient increase in chlorophyll *a* asso-

TABLE 1A. Annual primary production and mean chlorophyll *a* in Great Central Lake, B.C., 1970–76.

Year	Primary production ($g\ C \cdot m^{-2} \cdot yr^{-1}$) 0–10 m	Primary production ($g\ C \cdot m^{-2} \cdot yr^{-1}$) 0–30 m	Chlorophyll *a* ($mg \cdot m^{-2}$) 0–10 m	Chlorophyll *a* ($mg \cdot m^{-2}$) 0–30 m	Production/chlorophyll *a* (relative) 0–10 m	Production/chlorophyll *a* (relative) 0–30 m
1970[a]	11	21	7	25	1.57	0.84
1971	13	18	13	45	1.00	.40
1972	13	17	13	72	1.00	.24
1973	7	12	10	39	0.70	.28
1974[b]	4	7	6	28	0.67	.14
1975	5	7	7	47	0.71	.15
1976	7	14	7	29	1.00	.48
Mean						
[a]Treated	11	17	11	45	1.07	.44
[b]Untreated	5	9	7	35	.79	.26

TABLE 1B. Mean primary production and chlorophyll *a* in Great Central Lake, B.C., during June, July, and August.

Year	Primary production ($mg\ C \cdot m^{-2} \cdot h^{-1}$) 0–10 m	Primary production ($mg\ C \cdot m^{-2} \cdot h^{-1}$) 0–30 m	Chlorophyll *a* ($mg \cdot m^{-2}$) 0–10 m	Chlorophyll *a* ($mg \cdot m^{-2}$) 0–30 m	Production/chlorophyll *a* (relative) 0–10 m	Production/chlorophyll *a* (relative) 0–30 m
1970[a]	4.8	8.8	4.3	19.3	1.12	.46
1971	5.7	8.0	12.0	60.6	.48	.13
1972	4.6	7.2	14.5	131.7	.32	.05
1973	4.0	5.6	10.0	49.0	.40	.11
1974[b]	0.3	1.7	3.6	32.2	.08	.05
1975	1.0	3.9	5.5	56.7	.18	.07
1976	1.3	3.5	6.8	27.7	.19	.13
Mean						
[a]Treated	4.78	7.40	10.2	65.1	.58	.19
[b]Untreated	.87	3.03	5.3	38.9	.15	.08

ciated with *Rhizoselenia* sp. in 1972 bore no obvious relation to water chemistry. The algal accumulation, primarily in and just below the thermocline was very nonproductive, and was likely due to an accumulation of cells sinking from the fertilized layer and a lack of grazing on this genus.

The fraction of total production occurring in the upper 10 m was much greater in the years of enrichment. On four occasions indices of photosynthesis (^{14}C uptake) were measured in the upper 10 m on the day of fertilization and 4 subsequent days: production peaked on the 3rd d following enrichment, then declined (Table 2), indicating that production pulsed in accordance with the weekly additions. Production in the fertilized area was approximately double that in the unfertilized area (Table 3) and the difference was significant. Chlorophyll *a* concentrations also averaged higher in the fertilized zone, but the increase was not significant at the 5% level. Although production was less in the unfertilized area than in the fertilized area, it was, nonetheless, greater than production in the lake during untreated years (compare Table 1B with Table 3).

In 1971, we compared the vertical distribution of photosynthesis during deep injection of fertilizer with that in the unfertilized area (Fig. 2), and with that during surface application. Production in the unfertilized area was maximal at the surface and declined with depth (Fig. 2A), whereas in the area subject to deep fertilization maximum production was not only greater but was observed at the depth of nutrient injection, 10 m. Within the fertilized area the depth of maximum primary production changed from the surface to 10 m and back to the surface in accordance with changes in the depth of application of fertilizer (Fig. 2B).

Data from the summer of 1976, not yet fully analyzed, confirm the decrease in primary production observed in 1974 and 1975, after fertilization was stopped. The difference in primary production between treated and untreated summers appears too great to be attributed to natural events. Further analysis is required to

TABLE 2. Mean (daily) rate of primary production in Great Central Lake, B.C., during 5-d periods (nutrients added on day 1), for four trials.

	Day				
	1	2	3	4	5
Production (mg C·m^{-2}·d^{-1})	9.2	8.4	13.1	19.6	15.1
Production (relative to minimum mean)	1.1	1.0	1.6	2.3	1.8

TABLE 3. Mean primary production (observations on mean, n ≥ 10), in treated and untreated areas of Great Central Lake during June, July, and August.

	Fertilized area (mg C·m^{-2}·h^{-1})		Unfertilized area (mg C·m^{-2}·h^{-1})	
Year	0–10 m	0–30 m	0–10 m	0–30 m
1970	9.8	15.5	4.0	8.1
1971	4.4	10.5	2.4	5.7
1972	6.3	8.7	2.6	4.8
1973	4.7	6.4	3.2	4.8

H_0 (production in fertilized zone equals that in unfertilized zone) rejected, $0.001 < P < .05$, in each year, using Mann-Whitney test.

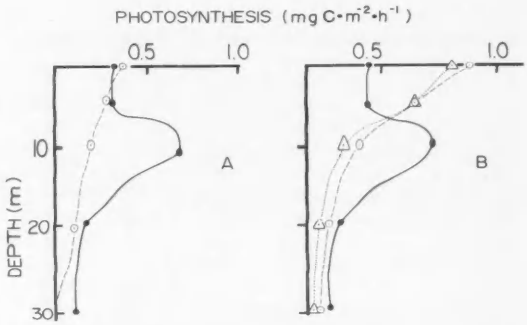

FIG. 2. A, Comparison of unfertilized station (○, $n = 7$) with deep fertilized station (●, $n = 12$) during period of deep injection of nutrients, 1971; B, deep fertilization (●, $n = 12$) compared with surface fertilization in early summer (○, $n = 9$) and late summer–autumn (△, $n = 6$), 1971.

explain the high winter production in 1976, for which the persistence of thermal stratification into December may be partially responsible.

The statistical significance of the difference in primary production in treated and untreated areas of the lake, the effects of deep fertilization on the vertical distribution of photosynthesis, the association of a weekly pulse in primary production with the weekly addition of nutrients, the higher ratio of primary production/chlorophyll *a* occurring with enrichment, and the change in partition of production in the 0–10- and 10–30-m depth ranges during treatment all substantiate the hypothesis that the summer increase in primary production was caused by nutrient addition. During June, July, and August of the fertilized years, nutrients in the epilimnion were usually very low and undetectable, consistent with the observation of pulsing of production in phase with the weekly additions. In the year following cessation of enrichment, nitrate remained detectable for a considerable portion of the growing season — probably a reflection of the very high nitrogen to phosphorus ratio (73:1 by atoms), i.e. phosphorus was limiting. However, the nitrogen was ultimately consumed, presumably in concert with phosphorus recycling. Thus it appears that the dynamics of nutrient availability was of greater significance than nutrient concentration per se.

Rates of utilization of added nutrients by phytoplankton were compared between years with the rate of fertilizer addition. This was done by converting the observed rates of primary production (expressed as carbon) during the periods of nutrient addition to nitrogen equivalents, i.e. rate of uptake or fixation of dissolved nitrate–nitrogen from the lake by phytoplankton. The fraction of the added nutrients utilized by the phytoplankton decreased between the first and last years of the experiment. The decrease was associated with an increase in the abundance of periphyton (attached algae) in the littoral zone of the lake. Quantitative observations on the periphyton were not made. However, while the increase in attached algae was readily apparent it did not become luxuriant. We speculate that the decline in utilization of the added nutrients resulted from competitive uptake by the increasing mass of periphyton. The significance of this possible competition for nutrients for juvenile sockeye salmon requires further study, particularly as such competition may relate to possible shifting in food chains that could affect their food supply.

ZOOPLANKTON

The literature dealing with the lake growth of sockeye salmon and zooplankton biomass commonly gives the average biomass for the growing season of the sockeye fry. In Great Central Lake, this growth period is April 15 through December 1. In the treated years zooplankton biomass during this period was substantially greater than during untreated years (Table 4). The mean biomass for the 3, post-treatment years was 0.87 ($S\bar{x}$ 0.08) g·m^{-2} and for the years with nutrient enrichment was 7.9 ($S\bar{x}$ 0.86) g·m^{-2}. The zooplankton biomass was increased nearly ninefold during treated years.

Zooplankton biomass increased most during the sum-

TABLE 4. Mean zooplankton biomass (g/m^2) in Great Central Lake from 50-m vertical net hauls.

		1969	1970	1971	1972	1973	1974	1975	1976
Jan. 1			0.7	3.1	2.3	2.0	0.4	0.2	0.2
15			0.7	1.7	2.1	1.3	0.3	0.2	0.3
Feb. 1			0.4	0.6	1.7	1.0	0.3	0.1	0.4
15			1.5	1.7	2.5	1.3	0.4	0.1	0.2
Mar. 1			2.2	1.6	2.3	1.7	0.4	0.1	0.3
15			1.3	1.3	2.0	2.1	0.6	0.2	0.2
Apr. 1			2.0	1.2	1.8	3.0	0.5	0.2	0.3
15			2.6	1.3	1.8	4.0	0.4	0.2	0.4
May 1			2.6	1.1	1.4	5.2	0.6	0.2	0.6
15		0.5	4.6	1.3	1.1	5.3	0.8	0.3	1.0
June 1		0.6	6.3	3.3	1.7	4.9	1.2	0.4	0.9
15		1.0	12.1	6.8	2.3	3.8	1.0	0.5	0.8
July 1		1.4	14.8	8.1	2.6	7.7	1.9	0.6	1.0
15		1.7	31.0	6.6	3.1	14.0	1.4	1.1	1.2
Aug. 1		1.7	32.7	8.9	3.8	22.5	1.3	1.2	1.5
15		1.4	18.0	12.6	4.4	8.2	1.4	0.6	1.9
Sept. 1		1.8	13.3	11.8	5.3	5.0	1.3	0.4	2.0
15		2.3	11.3	6.8	2.9	8.3	1.1	0.4	1.5
Oct. 1		2.8	15.2	6.8	3.5	4.7	0.8	0.3	1.2
15		2.9	19.1	10.0	7.6	8.8	0.2	0.2	1.2
Nov. 1		2.0	27.0	13.2	6.3	6.9	0.2	0.3	
15		0.5	8.6	9.6	2.0	4.5	0.2	0.3	
Dec. 1		1.2	1.5	7.0	3.2	3.1	0.2	0.3	
15		0.3	4.0	4.3	2.5	1.9	0.2	0.3	
"Biological Season"	Days								
Spring (Mar. 1–May 15)	75	—	2.5	1.3	1.7	3.6	0.5	0.2	0.5
Early summer (May 15–June 30)	45	0.9	9.4	5.2	1.9	5.4	1.2	0.4	0.9
Late summer (June 30–Sept. 2)	65	1.6	22.0	9.6	3.8	11.5	1.4	0.8	1.5
Summer (May 15–Sept. 2)	110	1.3	16.6	7.4	3.0	8.9	1.3	0.6	1.3
Fall (Sept. 2–Dec. 1)	90	1.9	13.7	9.3	4.4	5.9	0.6	0.3	1.5[a]
Winter (Dec. 1–Mar. 1)	90	1.0	2.0	3.2	1.9	1.0	0.2	0.3	—
Annual (Mar. 1–May 15, 1 yr later)	440	1.5[a]	8.4	4.9	3.0	4.5	0.6	0.4	—
Emergence and summer growth (Apr. 15–Sept. 2)	125	1.1[a]	12.6	5.8	2.7	7.7	1.1	0.5	1.1
Growing season (Apr. 15–Dec. 1)	200	1.4[a]	13.1	6.8	3.2	6.3	0.8	0.4	1.0[a]
Secondary production	395	7.8	64.0	67.8	27.2	27.8	4.1	3.2	—

[a]Data set incomplete.

mer and fall of treated years. Increase of zooplankton biomass from a March minimum to the summer maximum, ca. 135 d, was approximately 45% faster in the treated years than it was in the untreated years. The estimated daily instantaneous rates of biomass increase was 0.0178 and 0.0123, respectively.

Distribution of zooplankton was relatively uniform along the lake. This was attributed to the wind-dominated circulation (LeBrasseur and Kennedy 1972). Zooplankton were distributed throughout the 200-m water column, but less than 4% by weight were below 40 m. When the lake was thermally stratified, different species tended to be found at specific depth zones and diel migrations occurred within the respective depth zones. Consequently day and night catches within zones were similar. Forty-six percent of the zooplankton biomass was found in the upper mixed layer (ca. 0–10 m), 29% in the thermocline (ca. 10–20 m), and 20% from 20–30 m, while the remainder was distributed over the remaining 170 m depth.

The numbers of zooplankton species changed with treatment (Table 5). Considering all years, a total of 29 species was identified. Samples taken in 1969 (pre-treatment year) yielded a maximum of 10 species, while in the final year of treatment (1973) 22 species were found. However, the mean number of species per sample varied less: 7–10 species per sample in untreated years to 12 in the final year of treatment. During the post treatment period the number of species per sample declined, and in 1976 (not shown in Table 5) 14 species were identified. Throughout the period 1969–76, eight species (three copepod, two cladoceran, and three rotifers) persisted as numerical dominants (seasonal counts exceeding $1000/m^2$) in the zooplankton community. These species were reported earlier (LeBrasseur and Kennedy 1972). The number of species present in-

TABLE 5. Mean number of zooplankton species in Great Central Lake, from 50-m vertical net hauls.

Time period	1969	1970	1971	1972	1973	1974	1975
Dec.–Jan.–Feb.	—	8.1	7.3	9.2	10.5	10.0	6.7
March	—	8.3	7.0	9.0	7.5	6.7	4.5
Apr.	—	9.0	6.2	9.7	9.5	6.5	5.5
May	5.5	8.0	8.1	13.2	9.7	8.8	8.7
June	7.0	8.6	8.6	12.8	11.7	7.7	10.5
July	8.5	9.1	8.3	13.2	13.3	9.5	9.7
Aug.	9.5	9.3	9.4	11.0	14.2	12.0	10.5
Sept.	6.0	7.8	11.3	12.2	12.7	—	10.2
Oct.	5.0	7.9	12.1	11.0	11.7	—	12.7
Nov	7.0	8.0	12.5	11.7	10.7	7.5	11.2
$\bar{x}$	6.9	8.4	9.1	11.3	11.2	8.6	9.0
SE	0.6	0.2	0.7	0.5	0.6	0.7	0.8

May 1–Nov. 30

	Pretreatment	Treatment	Treatment	Posttreatment
$\bar{x}$	6.9	10.6	12.1	9.9
SE	0.6	0.4	0.3	0.5

Total species identified	1969	1970	1971	1972	1973	1974	1975	All years
	10	11	17	19	22	18	15	29

creased from late winter to the late summer and fall when the lake was warmest and well-stratified.

Rotifers accounted for most of the increase in the number of zooplankton species. Only 3 species occurred in 1969 but 11 were identified in 1973. Many of the invading species of rotifers were still present in the lake in 1976. All six endemic species of copepods, however, occurred with greater frequency in the samples during the period of nutrient additions. Fecundity of the copepods also increased. Cladocera were represented by three species at the onset of fertilization. One of these species disappeared from the samples and was replaced in equal abundance by two other species in the same genus by 1972. All three of these species were found in the lake in 1976.

The zooplankton community responded to nutrient enrichment by accelerating seasonal rate of increase in standing stock, in the size of this standing stock, and by increasing the number of species. These observations on the zooplankton community most appropriately describe the short-term changes in trophic conditions and should be supplemented by determining the time required for the community to revert to its prefertilization condition, if indeed that condition is recoverable.

We are tempted to speculate on the possible effect(s) of doubling the concentrations of nutrients being added, e.g. from 0.03 $g \cdot m^{-2}$ to 0.06 $g \cdot m^{-2}$ PO_4-P, on the zooplankton community. However, not all responses of the zooplankton were beneficial. As noted above, for example, the major structural change in the community involved the rotifer population, with respect to both their abundance and the number of species present. These organisms did not form a direct part of the sockeye food web. However, Sorokin and Paveljeva (1972) reported that in Lake Dalnee, where the rotifer community includes a predatory rotifer of a size that can be eaten by sockeye, this can lead to an efficient bacteria→protozoa→rotifer→predatory rotifer→sockeye food chain. This aspect could not be examined because a suitably sized predatory rotifer is absent in Great Central Lake. In addition, the incidence of parasitism and disease among copepod species increased during fertilization and subsequently decreased. Therefore, to maintain experimental nutrient additions at winter levels would seem to be the prudent course of continued experimentation.

JUVENILE SOCKEYE SALMON

The estimated egg depositions, which was calculated from the number, and sex ratio of adult spawners (Manzer 1976b), ranged from 25 to nearly 340 million during the study period (Table 6). The juvenile population in November was estimated from echo-

TABLE 6. Population statistics for juvenile sockeye in Great Central Lake, B.C.

	Year	Potential egg deposition and density: In millions	Egg/m²	Juvenile pop. November Estd. no. per 100 m²: 0+	1+	Σ	1+/0+ (%)	(%) survival to November 0+	Schedule of mean weights (mg): First spring 0+ fry	November 0+	Year +1 Second spring 1+ smolt	1+	November 1+	Year +2 Third spring 2+ smolt
Fertilization	1969	105	1.91	6.7	.08	6.8	1.2	3.0	156	1 050	2 800	1 107	6 600	9 030
	1970	108	1.96	21.6	.28	21.9	1.3	9.8	156	1 330	2 900	1 107	4 480	6 290
	1971	25.5	0.46	5.2	1.5	6.7	28.8	11.1	156	1 500	2 725	1 107	4 050	10 110
	1972	58.5	1.06	12.2	.46	12.7	3.8	10.3	156	2 000	4 200	1 107	6 100	14 300
	1973	143	2.60	33.1	.33	33.4	1.0	10.1	156	1 525	2 700	1 107	3 800	4 040
	1974	338	6.14	37.6	3.7	41.3	10.0	5.6	156	1 450	2 550	1 107	4 120	4 670
	1975	105	1.91	5.2	4.0	9.2	76.9	3.3	156	1 490	3 000	1 107	—	—
	1976	213	3.87	24.4	0.1	24.5	0.4	6.7	156	—	—	1 107	—	—

sounder surveys in conjunction with midwatertrawl catches (Robinson and Barraclough 1978). Estimated survival from potential egg deposition to the November estimates of juveniles per 100 m² of lake surface was <7% in the 3 yr after fertilization (3.3–6.7%) and about 10% (9.8–11.1%) in the 4 yr of fertilization (Table 6). Both estimated abundance, and relative numbers of age 0+ and 1+ sockeye varied widely from year to year depending upon the abundance of spawners (Table 6, Fig. 4). The maximum density of juvenile sockeye in November was 0.41 m^{-2} in 1974 and the minimum was 0.07 m^{-2} in 1969 and 1971, a sixfold range in numbers.

It is apparent that large sockeye differed from small sockeye in their distribution and availability to the trawl during the autumn sampling period. The samples appear to be biased towards the smaller size-groups (see Data Reports for samples). Consequently the abundance of larger age 1+ and 2+ juveniles may be underestimated. Beach seine catches and a series of inshore–offshore trawl catches indicated that the larger fish were not always available to the standard trawl tows made in midlake. Nevertheless, the ratios of age 0+ and 1+ sockeye in the fall tend to reflect the relative proportions of these age-groups sampled as smolts the following spring at a weir where gear selectivity was not a factor. Net avoidance by larger sockeye under certain light intensity conditions, e.g. full moon, may also bias population estimates, but the year-to-year abundance and ratio of 0+ to 1+ juvenile sockeye appears to be adequately represented by trawling and echosounder surveys (Robinson and Barraclough 1978).

Some of the fish aged as 2+ smolts may actually be 3+ yr of age. The difficulty of ageing arises, in part, from the long period of fry emergence and uncertainties about the time of annulus formation. For at least some of the fish an annulus was not laid down every year. Reexamination of selected 2+ smolt scales indicates

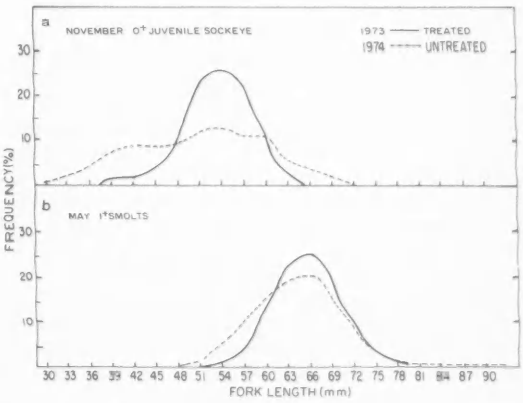

FIG. 3. Length-frequency distribution (%) for juvenile sockeye (0+) in November and May (1+) for a treated and an untreated year. a, November 1973, 0+, $n = 1{,}163$; $\bar{m} = 53.6$, $S\bar{x} + 0.13$; b, November 1974, 0+, $n = 2{,}410$; $\bar{m} = 50.9$, $S\bar{x} = 0.18$; May smolts — (see Table 7).

<10% of the migrants could ultimately be reclassified as 3+. The effect of increasing the age of some fish would be to reduce the mean weight of 2+ smolts shown in Table 6 by a maximum of 2 g for some years.

The initial weight of age 0+ sockeye fry in the spring was assumed to be constant from year to year and was assumed equal to the size of the smallest fish caught. The weight of sockeye at other periods was determined during their lake residence from trawl samples and samples of migrating smolts. The mean weight of sockeye from the time of hatching to seaward migration as a 1- or 2-yr-old smolt can be seen by reading across Table 6. With the possible exception of 1975, most sockeye spent only 1 yr in the lake; consequently

TABLE 7. Mean fork length (mm) of 1-yr old sockeye smolts leaving Great Central Lake, 1969 to 1976. (SE = standard error of the mean).

			Treated					
	1969	1970	1971	1972	1973	1974	1975	1976
No. sampled	781	1332	7503	2408	4516	5426	5197	1688
$\bar{x}$	67.5	70.61	70.19	66.54	77.75	66.52	64.29	68.82
SE	0.15	0.16	0.08	0.09	0.09	0.06	0.08	0.13
Range	54–80	52–83	51–101	52–83	59–104	50–86	48–94	52–85

only a minor fraction of most year-classes experienced more than 1 yr of nutrient treatments.

Although the 0+ sockeye in 1972 were the largest measured during the fall period and these fish in turn produced the largest 1+ smolts, there was no general relationship between size (length or weight) in the 1st yr of lake residence and subsequent smolt size for the other years. Nor did the number of fish of a particular age-group and their subsequent average size appear to be related. With the exception of 1972, the weights of 1+ smolts were remarkably constant from year to year, dispelling the expectation that increased nutrients would act through the food chain to produce larger smolts. The weight of 2+ smolts, "holdovers" during fertilization, however, was approximately double that of untreated smolts of the same age in years of no fertilization (9.95 g ± 1.67 and 4.3 g ± 1.05, respectively). The number of 1+ "holdovers" sampled as in-lake juveniles was small.

Sockeye from the 1972 brood year experienced fertilization in 1973, those from the 1973 brood year did not. Estimated abundance during November in each year was comparable (33.1 and 37.6 per 100 square metres, respectively, Table 6). In 1973 sockeye as age 0+ fish in November exhibited a normal-type length-frequency distribution (Fig. 3a). Under untreated conditions in 1974 sockeye as 0+ fish exhibited a platykurtic distribution (Fig. 3a). Approximately 29% of the 0+ sockeye in 1974 were smaller than their counterparts in 1973 and about 7% were larger (Fig. 3a). By the time of emigration as smolts the differences between the length distributions of the 2 brood yr had declined to 15% smaller and 1% larger (Fig. 3b), but fish from the 1973 brood were still smaller. The mean range in lengths of smolts was quite variable for most of the years sampled (Table 7).

The biomass of sockeye juveniles per unit area of lake surface during different seasons was calculated from the November estimate of abundance and monthly samples of fish together with estimates of instantaneous growth rate and annual rations (Table 8). The biomass inventories are the product of population estimates of 0+ and 1+ sockeye in the lake in November and average weight of sockeye sampled during the growth year. For the purposes of calculations, all mortality was assumed to take place prior to the fry feeding, i.e. in the egg and alevin stages. The number of fish observed in the lake was assumed to be constant from May to the following spring prior to smoltification and equal to the November population estimate. This assumption is in conflict with other studies on mortality rates for juvenile sockeye which show mortality occurring throughout the year (Ricker and Foerster 1948). However, in the absence of data we have simplified calculations for growth parameters of the fish. Population estimates made monthly from July through December suggest that the survival is close to 100% during this period (Robinson and Barraclough 1978).

Although mortality probably occurred throughout the growth year, recruitment of fry was sufficiently extended and extensive in the summer that an overall change in population size was not detectable. Data on population size from December to out-migration the following spring are sparse, partly because of ice cover on the lake and partly because the efficiency of the trawl decreased as the fish increased in size. The numbers of smolts are assumed to be made up of the November 0+ and 1+ age-groups minus those fish remaining in the lake as holdovers for a 2nd yr. The estimate of rations is based upon Winberg's (1956) equation where the ration is expressed as a simple relation between growth and metabolic rate. The latter was calculated on the basis of an average temperature of 10°C and the geometric mean of the fish weight during the respective time intervals. The assumption of no mortality will overestimate the ration requirements but these estimates can be expected to be within an "order of magnitude" of the sockeye food requirements. The biggest source of error lies in the assumption of no mortality during lake residency.

The highest relative annual rate of biomass increase (.80 in 1972) was almost double the lowest (.47 in 1975) (Table 8). These extremes were achieved with closely similar annual rations, 2.1 and 2.2 $g \cdot m^{-2}$. The estimates (Table 8) suggest that annual food cosumption reflected numbers and biomass of sockeye, rather than relative growth rate.

Barraclough and Robinson (1972) reported that young sockeye fed mainly at two times during their diel migration. Feeding occurred primarily during twilight

TABLE 8. Estimated seasonal biomass, instantaneous growth rates, and annual food consumption for juvenile sockeye in Great Central Lake.

	Sockeye biomass			Instantaneous rate of biomass increase		Estimate of annual rations
	0+	1+	Σ	Seasonal	Annual	
	(mg·m⁻²)			(K × 100)		g·m⁻²
1969						
Spring	11.3	0.9	12.2			
Summer						
Fall					.72	0.8
Winter and spring	203.1	4.8	207.9			
1970						
Spring	33.9	2.9	36.8			
Summer	195.9	12.3	208.2	1.24		
Fall	289.5	19.4	308.9	0.44	.73	2.6
Winter and spring	631.2	26.6	657.8	0.46		
1971						
Spring	7.9	20.3	28.2			
Summer	39.3	48.2	87.5	.81		
Fall	75.6	72.0	147.6	.58	.54	1.3
Winter and spring	137.3	101.1	238.4	.29		
1972						
Spring	20.0	5.1	25.1			
Summer	106.6	11.3	117.9	1.1		
Fall	256.9	19.8	276.7	.95	.80	2.1
Winter and spring	539.4	49.6	589.0	.46		
1973						
Spring	49.4	3.9	53.1			
Summer	240.1	13.3	253.4	1.11		
Fall	483.0	21.5	504.5	.76	.72	3.7
Winter and spring	855.0	50.5	905.5	.35		
1974						
Spring	56.6	44.5	101.1			
Summer	312.1	128.6	440.7	1.05		
Fall	526.3	152.7	679.0	.48	.60	5.4
Winter and spring	925.5	162.4	1087.9	.29		
1975						
Spring	8.6	47.5	56.1			
Summer	22.0	155.0	177.0	.82		
Fall	81.8	176.9	258.7	.42	.47	2.2
Winter and spring	164.7	200.5	365.2	.21		

periods and in the epilimnion on adult zooplankton. Secondary feeding activity occurred at dawn as the fish return to daytime depths. No feeding occurred during darkness at any time of the year. Larger fish ate more food but the relative weight of stomach contents decreased with increasing body size and age. The stomach contents usually amounted to <3% of the body weight for age 0+ fish, 1% for age 1+, and about 0.5% for 2+ and 3+ fish.

Little feeding was observed in fry during their first 2-wk period after their emergence in April. By May the average stomach contents was about 4% of their body weight. This amount decreased to 2% from June to August and rose again to 3% in September and October in some years, then decreased to about 1% from November to March in the next year. The contents for age 1+ fish varied from 0.5 to 1.5% seasonally, averaging 1% of the body weight as reported above. Pronounced seasonal diversity in the predominant dietary items tended to reflect the dominant member(s) of the zooplankton community.

Cyclopoid copepods were an important component in the diet throughout the year but their relative importance varied greatly from month to month and from year to

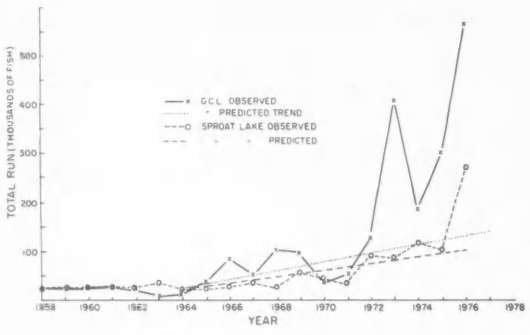

FIG. 4. Total adult sockeye returns to Great Central Lake and Sproat Lake (commercial catch and escapement) 1958–76. x, Observed Great Central Lake returns; - - - - -, predicted trend line; o, observed Sproat Lake returns; . . . . . ., predicted trend line.

year. From late summer to late fall insects formed a minor part of the diet (3%); they did make up as much as 10% of the diet by weight in 1970.

Chironomids were a frequent dietary constituent during the late winter–early spring, forming 100% of the diet during some winter periods, although they were infrequently found in large quantities in zooplankton samples.

The diet of age 1+ sockeye, was similar to that of the underyearling sockeye throughout the year, with one exception. The two smaller zooplankton species, *Cyclops* sp. and *Bosmina* sp. formed relatively minor portions of the diet of 1+ juveniles in all years except in late summer and fall of 1974. During the first post treatment year, smaller zooplankton species formed 60% of the diet of the age 1+ juveniles. Chironomids were more important in the diet of the age 1+ fish particularly in the winter months and early spring. Larval fish (*Cottus* sp.), which occurred only occasionally in the age 0+ fish, made up a more significant part of the diet of the 1+ fish during the summer months, and in June 1970 fish larvae made up over 60% by weight of their diet.

Laboratory observations on juvenile sockeye by Brett et al. (1969) indicated that water temperatures between 5 and 17°C were optimal for conversion efficiency and growth. The observed vertical distribution of the sockeye in Great Central Lake indicates that the fish tended to avoid temperatures <4 and >18°C. Echo-soundings indicate that the fish were distributed at depths between 40 and 100 m during daylight, with highest concentrations at the 60-m depth interval. One hour after sunset the sockeye would be concentrated in a layer of 12–30 m thickness at depths between 4 and 40 m depending upon the season. Only during the early winter and the spring migration were juvenile sockeye caught at the surface, and the fish were otherwise rarely,

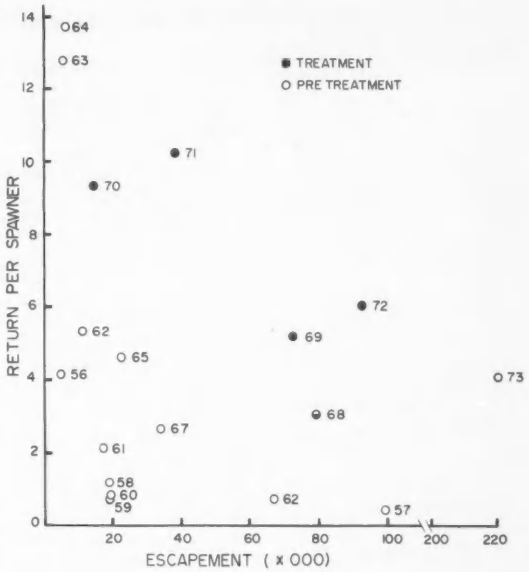

FIG. 5. Relationship between escapement size and return per spawner, 1956–73. Numerals associated with datum point indicate brood year.

if ever, at the surface (Barraclough and Robinson 1972). From July through September, when epilimnial temperatures exceeded 17°C, the sockeye apparently made little if any direct use of the zooplankton in the epilimnion where approximately half the zooplankton biomass was concentrated (LeBrasseur and Kennedy 1972). Thus, during the season of maximum temperatures, one might assume that only half of the zooplankton standing stock is available to sockeye.

SOCKEYE ADULTS

Partition of 1976 returns between the two lakes is provisional and incomplete. Mean returns of untreated sockeye to Great Central Lake between 1958 and 1972 inclusive were about 52 340 fish (±12 000 or 23% SE). Corresponding returns of treated fish (1973–76) were about 373 058 (±89 000 or 24% SE). Corresponding returns to Sproat Lake are estimated to be 31 530 (±3700 or 11.6% SE) and 129 017 (±16 000 or 13.9% SE). The returns of treated fish to Great Central Lake averaged about 6.7 times greater than untreated fish. The corresponding factor for returns to Sproat Lake was 4.1.

However, if the estimated total annual sockeye return to each lake is examined for the period 1964 through 1972 an upward trend is evident (Fig. 4). Extrapolation of the trend line through the period of treated adult returns to Great Central Lake suggests

TABLE 9. Reproductive success of Great Central and Sproat lakes sockeye salmon for untreated (1966–67) and treated (1969–71) runs. R.I., reproductive index.

Year	Great Central			Sproat			
	Parent (a)	Progeny (b)	$\frac{b}{a}$ = R.I.	Parent	Progeny	R.I.	Sproat/G.C.L.
Untreated							
1966	62 000	41 000	0.66	17 000	40 500	2.38	
1967	33 000	88 000	2.67	22 000	44 400	2.02	
Mean R.I.			1.67			2.20	1.31
Treated							
1969	73 000	371 000	5.08	24 000	95 000	3.96	
1970	15 000	130 000	8.67	18 000	109 500	6.08	
1971	39 000	328 000	8.41	25 000	107 500	4.30	
1972	93 000						
Mean R.I.			7.39			4.78	0.65
Treated R.I./Untreated R.I.			4.43			2.17	0.49

that treated age classes benefited by 1.6–4.4 times (average for 4 yr of treated returns is 3.1). Similarly, if the trend line for Sproat Lake is extended for 1973 through 1976, then it is apparent that 3 of the 4 yr were not significantly different from what might have been realized. However, the sockeye stocks identified as Sproat Lake fish in their 4th yr (1976) were 2.6 times more abundant than the predicted return of 100 000 fish based upon linear regression analysis of the trendline.

Indices of reproductive success (return per spawner) (Fig. 5) suggest that the return per spawner was higher for the treated brood years. The mean increase in reproductive success derived from data on treated and untreated runs of comparable size (15 000, 39 000, 73 000, 93 000) was calculated to be about fourfold (4.4).

Returns per spawner for Sproat Lake brood years, 1969-1972, corresponding to treated Great Central Lake broods, were more than double the values for the 1966 and 1967 Sproat brood years (Table 9). However, the relative increase in corresponding estimates of Great Central Lake reproduction success was twice that for Sproat Lake.

Historically, the variability (SE = 23%) of returns to Great Central Lake have been substantially higher than in Sproat Lake (SE = 12%). We speculate (Manzer, 1976b) that the substantially increased smolt runs from Great Central Lake worked to decrease depensatory mortality factors, e.g. predators common to smolts migrating from both lakes. Other possible explanations for the simultaneous improvement of adult returns to Sproat Lake might include (1) cultural eutrophication in recent years acting to improve sockeye food supply in Sproat Lake, (2) supplementation of escapement to Sproat Lake by Great Central Lake spawning stock (straying), and (3) population expansion into hitherto underutilized rearing environments due to historically low escapements. The possibility of straying by Great Central Lake sockeye is not supported by the literature or by biometric characteristics of the two stocks. However, such factors singly or in combination could account for the increase in sockeye to Sproat Lake.

The substantial increase in Great Central Lake adult sockeye returns coincident with the fertilization program is of sufficient magnitude to render most difficult attempts to discount fertilization as the major causal factor.

Discussion and Conclusions

Four summary statements describe the results of the lake enrichment experiment and set the stage for general discussion and conclusions:

i) The annual rate of primary production in the upper 30 m of Great Central Lake during years of fertilization averaged 17 g C·m^{-2} compared with 9 in the 3 yr following fertilization. May through August production in treated years was 5 times greater than in untreated years. Several lines of evidence support the hypothesis that the increase in primary production was caused by the controlled enrichment.

ii) The mean biomass of zooplankton present in the lake during the season of most active feeding by juvenile sockeye was increased about 9 times during treated years. The numbers of species identified from the samples also increased, with some of the additional species being of direct benefit to the sockeye. On cessation of treatment species diversity and zooplankton standing stock declined.

iii) The growth of age 2+ smolts and the survival of

TABLE 10. Productivity coefficients for Great Central Lake, B.C. (from Tables 1, 4, 6).

Year		Zooplankton productivity / Primary productivity (1)	Zooplankton productivity / Zooplankton biomass (2)	Zooplankton ration for fish / Zooplankton productivity (3)	Fish productivity / Zooplankton productivity (4)
		%	%	%	%
1969		—	5	25	3
1970		20	8	4	1
1971		25	14	2	0.35
1972	Treated	10	9	8	2
1973		14	6	14	3
1974		4	4	125	25
1975		3	6	71	11

age 0+ sockeye were increased during the period the lake was being enriched.

iv) The average returns of adult sockeye salmon subject to treatment increased by a factor of about 7, from about 50 000 fish to over 360 000 fish. Concurrent increase in run size and in reproductive success in neighboring untreated Sproat Lake were less than in Great Central Lake.

We recognized at the outset of the experiment that we would be unable to identify or measure the effects of all possible factors influencing fish productivity, i.e. total ecosystem analysis. However, while a host of factors in complex interplay could account for increased fish production in the system, such complexity should not obscure the trophic adjustments that ultimately allow for increased fish production. We expected each trophic level would exhibit a complementary response to the addition of nutrients. Indeed, such was the case. During the period of treatment, productivity parameters at each trophic level increased in magnitude beyond that observed for untreated periods. Notwithstanding these substantiative general findings, the task of indentifying and assessing specific food-chain linkages to account for increased productivity at each trophic level remains. Factors such as sunlight, temperature, flushing, species composition, population size of predator and prey, etc. need to be isolated and examined on a year-by-year basis rather than by combining several years' data.

The interrelations summarized in the present report between the different "links" do not appear wholly consistent. For example, the population size of juvenile sockeye in 1974 was the greatest observed. This was a direct result of a carry-over of age 1+ sockeye (ca. 2×10^6), and a large production of fry (ca. 21×10^6) resulting from an increased escapement (216 000) in 1973. Further, both summer primary production and zooplankton biomass were notably lower during 1974 than in treated years. One could speculate that the fish population was aproaching a density (ca. 0.5 fish/m^2) in 1974 capable of measurably limiting the zooplankton standing stock. Even if this were the case, other factors appeared to operate to mollify effects on fish carrying capacity of the lake. For example, the estimated age 0+ population in November 1974 experienced a high survival rate (6.14% potential egg deposition) though summer primary productivity and zooplankton standings stock levels were low, relative to treated years.

Some aspects of the phytoplankton–zooplankton–sockeye interactions were calculated from the data presented in Tables 1, 4, and 6 and are shown in Table 10. Various assumptions made in these calculations include factors for conversion to common biomass units (carbon), duration of the annual growing season, zero mortality after November for sockeye populations, constancy of biological rates and efficiency coefficients for different seasons, years, and species, etc. In addition, zooplankton production was considered equivalent to the instantaneous increase (decrease) in zooplankton biomass. However, the increase in biomass is related to the sum of growth and recruitment minus the combined effects of mortality and emigration for the various species contributing to the biomass. The data for recruitment, mortality, and emigration are not available for summarizing all species and years. Consequently a more precise discussion of zooplankton production is being deferred to a separate report. The values reported here should be considered conservative.

In years when the zooplankton biomass was relatively high (1970, 1971, and 1973), production of phytoplankton carbon per square metre amounted to about 20–30 mg for each milligram of carbon of zooplankton (Table 10). The chlorophyll *a* values in 1972 were exceptionally high due to the presence of a large biomass of *Rhizoselenia* sp., on which herbivorous zooplankton have difficulty grazing (Parsons et al. 1967). The low ratios of secondary to primary production observed for the untreated years 1974 and 1975 were associated with reduced phytoplankton production. With the drop in primary production between the treated period and 1975 (untreated) the ratio of apparent zooplankton production to primary production decreased from 10-25% to 3%. The decrease is consistent with observations by Cushing (1970), McAllister (1972) and Steele (1965).

The turnover rate for zooplankton, i.e. ratio of annual zooplankton production to annual zooplankton biomass, is remarkably uniform despite substantial year-to-year variations in both parameters. The extent to which production exceeds standing crop (4–14 times) is higher than that reported by Winberg (1971) from the Russian literature (2–6 times). However, the turnover ratio is influenced very much by the life histories of the dominant organisms in the zooplankton community. Thus organisms that are multivoltine and/or have a number

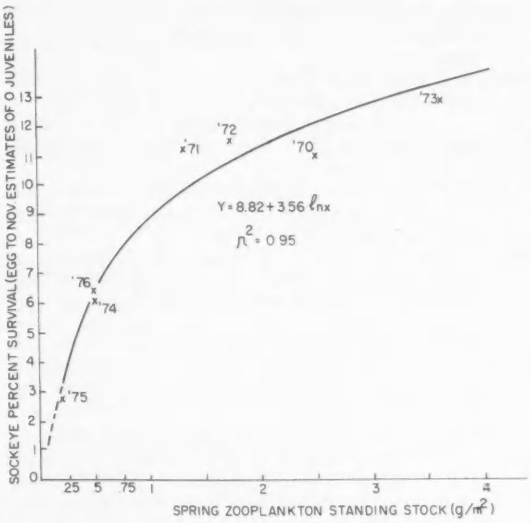

FIG. 6. Relationship between estimated survival (%) from potential egg deposition to juvenile sockeye in the following November and spring zooplankton biomass ($g \cdot m^{-2}$). Numerals by datum points refer to year of sampling.

of broods each year, i.e. Cladocera, might have annual production rates that exceed the standing stock by 10 or more (Waters 1969). The estimated rations relative to zooplankton production suggests the food supply for young sockeye was adequate, or even in excess during treatment years. However, it may have been inadequate during untreated years with large populations of juveniles. In 1974, estimated rations exceed zooplankton production by 25%. The ratio of fish production to zooplankton production suggests an adequate, if not oversupply, of zooplankton in treated years or, alternatively, that the lake could serve as a nursery area for a larger sockeye population. Spearman Rank correlation for columns 2 and 3, and 2 and 4 (Table 10) are inversely correlated at the 5% level. The data in columns are not independent and therefore correlation is to be expected. The ratios are useful, however, for comparisons with similar data for other lakes.

A relationship between factors that produce zooplankton, fish rations, and fish flesh is to be expected on biological grounds; however, the method of estimating ration and sockeye production relies heavily on the same data. Consequently, it is not demonstrable from this analysis of the data if there is a cause-and-effect relationship, if fish and zooplankton are responding in a similar manner to some common environmental factor, or if an artifact in the analyses is producing significant results. No correlation was apparent between production biomass ratios for phytoplankton and zooplankton (P/chlorophyll *a*, P/Z). However, coefficients for phytoplankton production and biomass from Table 1 and coefficients for secondary to tertiary production in Table 10 are significantly correlated. In this instance the apparent relationship is independent of the method of analysis, but as above, primary, secondary, and tertiary production could be responding similarly to a common factor such as the climate.

Annual growth rate and biomass per square metre for young sockeye showed no significant correlation with annual zooplankton production or biomass. The explanation suggested above was that zooplankton was generally in excess of the requirements for the numbers of fish in the lake or that a substantial portion of the zooplankton was unavailable to the fish.

The coefficients for zooplankton and fish production indicate that from 4 to 285 mg of zooplankton resulted in 1 mg of sockeye. The former value indicates a transfer efficiency of 25% while the latter is <1%, the average for all years being 2%. If the value of 10% efficiency found in the general literature is accepted, then it is apparent that food supply as calculated here was seldom limiting. The estimate of the ration required to produce the biomass of migrants yields comparable results, i.e. comparing the zooplankton produced to that required by the fish for metabolism and growth indicates that during treatment years <15% of the zooplankton was required by the fish, whereas in untreated years 25–125% was required. These data suggest that the lake could have supported more young sockeye during the years of fertilization. We speculate that for the rate and level of fertilization applied the lake could support 15–20 million juvenile sockeye. An adult escapement of approximately 100 000 would be required to produce this number. This projected carrying capacity remains tenable even though half of the summer zooplankton stock would be in the warm epilimnion and unavailable to feeding sockeye during the summer. The discrepancy between concentration of zooplankton in the epilimnion and the concentration of fish feeding in the thermocline has been noted earlier.

Laboratory evidence suggests that availability of food rather than the total amount produced can limit fish feeding (Ivlev 1961). In Great Central Lake we observed that most zooplankton were produced in the epilimnion, a region that young sockeye seemingly avoided when water temperatures exceeded 15–18°C. Furthermore, the weight of stomach contents expressed as a percentage of the body weight of sockeye underwent seasonal changes, being greater in the spring and fall than during the summer. Consequently, the statement that annual production of zooplankton during fertilized years was not fully utilized should be qualified by noting its markedly reduced availability to fish. Also, food preferences by the fish may influence their food intake. Strategies for increasing food availability to young sockeye, such as decreasing the epilimnial temperature in the summer and increasing the production of food organisms in the fall, could be tested to observe their effect on fish productivity.

Survival of age 0+ sockeye appears logarithmically related to spring (1 March–15 May) zooplankton biomass (Fig. 6). Zooplankton biomass levels above 1500 $mg \cdot m^{-2}$ appeared to have little additional effect

on survival rate of underyearling sockeye in Great Central Lake. A biomass of 1500 $mg \cdot m^{-2}$ is equivalent to 30 $mg \cdot m^{-3}$ or approximately four adult copepods (*Cyclops* sp.) per litre. A 156-mg sockeye fry could require food equivalent to 20% of its body weight per day or ca. 31 mg/d. Thus, average zooplankton populations of the order of 1–2 $g \cdot m^{-2}$ would appear adequate to meet the food requirements of the sockeye provided the zooplankton population is capable of replacing losses through predation and/or the number of feeding fish was too small to significantly reduce the zooplankton. When the zooplankton biomass was 250 $mg \cdot m^{-2}$ (5 $mg \cdot m^{-3}$, i.e. <1 *Cyclops* sp. per litre), the fish must obviously search a much larger area to obtain a daily ration, and under such conditions the number of prey may very well limit the survival of juvenile sockeye. The view that survival of newly emerged fry and food supply are related has received considerable support (Ivlev 1961; Braun 1967). However, it is not yet clear from the available data for Great Central Lake if a common factor such as an early spring could affect both fish survival and zooplankton biomass. Starvation and feeding experiments with newly hatched fry together with information on the extent to which littoral and pelagic zones are utilized by fry during the first few weeks of lake residence would help to establish the importance of food concentrations for early survival of sockeye fry.

Acknowledgments

We thank the many persons and agencies who have cooperated to make the lake fertilization project possible; particularly Port Alberni City Council, MacMillan Bloedel Ltd., B.C. Hydro and Power Authority, Department of Fisheries, Mr and Mrs H. Ostrander, and Mr J. Baker. In addition, we appreciate the scientific comments offered by many of our colleagues. Drs M. Healey and J. Mason were unstinting in their efforts to improve the manuscript; the responsibility for the remaining errors and omissions lies with the authors. We also benefited from the limnological experience and insights of Dr J. Stockner in his review of this manuscript.

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Appendix 1

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Daily Ration of Yellow Perch (*Perca flavescens*) from Lake Memphremagog, Quebec–Vermont, with a Comparison of Methods for In Situ Determinations[1]

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NAKASHIMA, B. S., AND W. C. LEGGETT. 1978. Daily ration of yellow perch (*Perca flavescens*) from Lake Memphremagog, Quebec–Vermont, with a comparison of methods for in situ determinations. J. Fish. Board Can. 35: 1597–1603.

In situ estimates of daily ration for yellow perch (*Perca flavescens*) range from a high of 5.5–6.7% body weight in July to a low of 2.2–2.4% body weight in October. The seasonal pattern corresponds well to known patterns of growth. Comparison of three methods for in situ determination of daily ration levels indicated the method outlined here and the more complex method of Thorpe yield similar results. The method of Keast and Welsh and derivatives of this method which correct for digestion between sampling periods give unreliable values that are 50% below the other two and, in general, are below maintenance ration levels. Diet composition and feeding activity varied seasonally and with body size.

Key words: body size relationships, diet composition, seasonality

NAKASHIMA, B. S., AND W. C. LEGGETT. 1978. Daily ration of yellow perch (*Perca flavescens*) from Lake Memphremagog, Quebec–Vermont, with a comparison of methods for in situ determinations. J. Fish. Board Can. 35: 1597–1603.

Les estimations in situ de la ration quotidienne des perchaudes (*Perca flavescens*) se situent entre un sommet de 5.5 à 6.7% du poids corporel en juillet à un creux de 2.2 à 2.4% du poids corporel en octobre. Quand on compare trois méthodes de détermination in situ des rations quotidiennes, on constate que la méthode décrite ici et la méthode plus complexe de Thorpe donnent des résultats semblables. La méthode de Keast et Welsh, et les méthodes qui en sont dérivées, tenant compte de la digestion entre les périodes d'échantillonnage donnent des valeurs douteuses qui sont de 50% inférieures à celles des deux autres méthodes et, en général, au-dessous des rations de subsistance. La composition du régime alimentaire et les activités liées à l'alimentation varient avec les saisons et la taille.

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THE application of laboratory-derived energy budgets for fish (e.g. Brett 1976; Solomon and Brafield 1972) to natural populations has been impeded by problems associated with in situ determinations of daily ration. Daily ration is defined as the total quantity of food consumed by an organism expressed as a percentage of its body weight. In situ estimates reported to date suffer from being limited to a specific size-class or calculated during a short period of time within the seasonal period of active feeding (Keast and Welsh 1968; Seaburg and Moyle 1964; Thorpe 1977). In addition, several of the in situ estimates of daily ration reported to date are at or below laboratory-derived estimates of maintenance requirements for the species at equivalent temperatures (Fortin and Magnin 1972; Keast and Welsh 1968; Popova and Sytina 1977; Seaburg and Moyle 1964).

To date Thorpe's (1977) method of determining in situ daily ration remains the only accurate one available; however, it is too time-consuming to be employed regularly in the field. Thus a need exists to determine a simple method that can accurately estimate natural daily consumption of food. We report herein our calculation of in situ food consumption by perch together with a comparison of results obtained using our method and two other methods currently in use (Keast and Welsh 1968; Thorpe 1977).

Materials and Methods

This study examined the feeding habits of yellow perch in Lake Memphremagog, Quebec–Vermont (45°06′N, 72°17′W) located 120 km east of Montreal (Fig. 1). The lake has three morphometrically distinct basins. Physical and biological characteristics are given in detail in Dermott et al. (1977), Gascon and Leggett (1977,) Nakashima and Leggett (1975), and Ross and Kalff (1975).

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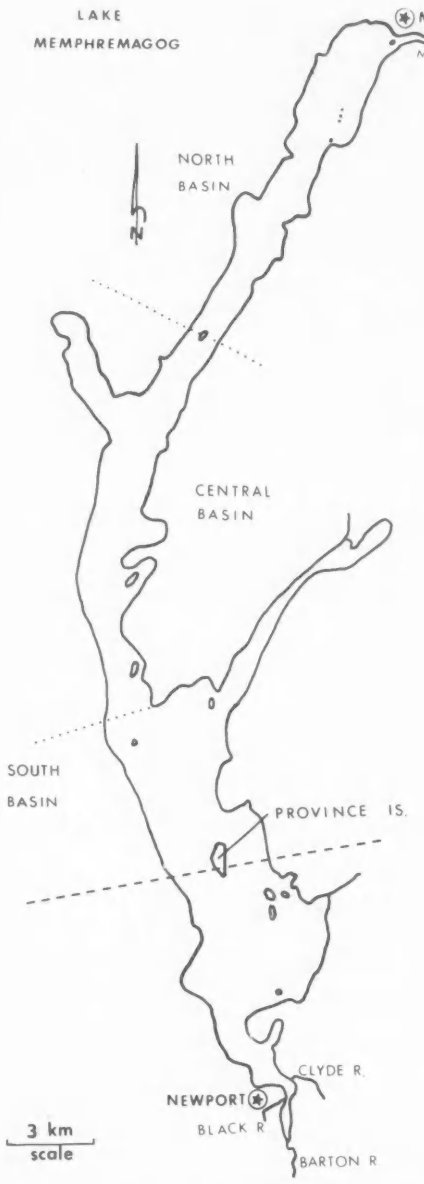

FIG. 1. Study area.

All sampling was conducted in the southern basin within a 1-km radius of Province Island, located on the Quebec–Vermont border. Mark–recapture studies undertaken by Nakashima and Leggett (1975) demonstrated that the perch of Lake Memphremagog do not undertake extensive movements. The fish sampled in this study are thus considered to have come from a homogeneous population. The physical and biological environment in the area is also quite uniform, thereby minimizing variance in feeding patterns that might be related to local habitat differences.

To determine daily ration levels we sampled 60–80 perch (fork length 83–310 mm) at 3-h intervals (mean fishing time 2.1 h, range 1.3–3.0 h) over two 48-h periods (July 7–9 and August 6–8, 1975) and three 24-h periods (September 4–5, October 5–6, 1975 and June 9–10, 1976). Sampling intervals were kept short to minimize the possibility of food being eaten and evacuated during the time the nets were fishing.

All fish were captured in experimental gill nets having five mesh sizes (2.54-, 3.81-, 5.08-, 6.35-, and 7.62-cm stretched mesh), each panel being 1.8 m deep and 15.2 m long. Nets were set on the bottom. Fish were placed on dry ice immediately after capture to halt digestion and prevent loss of body moisture.

In the laboratory, each fish was measured to the nearest millimetre fork length and weighed to the nearest 0.1 g. The contents of the stomach and intestine were removed and weighed separately and all stomach items were identified at least to order, and to family or genera where possible. The relative contribution of each food category to the total stomach content was estimated using the points method of Hynes (1950). Diet composition was determined by analyzing the stomach contents of all fish, sampled within 3 h of major feeding peaks, whose stomachs were at least ¾ full (Fig. 3). Food items were combined into six categories representing the major components of the diet (chironomid larvae, chironomid pupae, cladocera, ephemeropteran larvae, decapoda, and pisces). A seventh miscellaneous category incorporated food eaten only occasionally or confined to specific age-classes of fish and/or times of the year (Amphipoda, Chaoborus, Corixidae, Mollusca, and Trichoptera). Following analysis of the diet it was found that the perch could be divided into three size categories (83–150 mm, 151–200 mm, and 201–310 mm) based on the relative similarity of their diets. We thus estimated daily ration independently for each of these size-classes.

To estimate daily ration the total wet weight of the digestive tract (stomach and intestine) contents of all fish in a given size-class was summed and expressed as a percent of the total body weight of all fish in that size-class. This was repeated for each 3-h sampling interval. These values were then plotted against time and the percentages determined for the peaks of feeding activity (as determined from the plots) were summed to provide an estimate of food consumption during a 24-h period. This method assumes any food consumed in the interval between sampling remains in the stomach or intestine at the time of capture.

In most cases distinct feeding peaks were apparent (Fig. 3) and the minimum time between peaks was 8 h. Two exceptions occurred with the 151–200-mm size-class in June and the 201–310-mm size-class in July where the apparent peaks were separated by only 6 h. For consistency, we defined the next sampling point as the peak. The statistical effect of this choice was insignificant since the difference in ration level between the two possible points on each sampling date was $<0.5\%$. A further exception occurred with the 201–310-mm size-class sampled during the latter half of the 48-h in August where three minor peaks were recorded between 0900 and 2000 h. In this case the first and last of these were selected as peaks because of their correspondence with the timing of distinct peaks in the other size-classes and sampling intervals.

Some fish may have evacuated a portion of their stomach

contents into the intestine while in the gill nets. We therefore included the weight of the contents of the intestine in our calculation. Other investigators have either neglected this factor (Keast and Welsh 1968) or attempted to correct for the loss in stomach contents by employing a "compensation factor" (Fortin and Magnin 1972; Thorpe 1977).

Food is consumed by fish between sampling intervals and must be accounted for in the final estimate. Thorpe (1977) adjusted for this by using a correction factor assuming that the rate of food intake between samples was linear. In our method, we have included the food by weighing the entire digestive tract, thus eliminating the need to determine a correction factor.

To assess the relationship between daily ration and growth, the specific growth rate

$$G = \frac{\ln y_{t_2} - \ln y_{t_1}}{t_2 - t_1} \times 100$$

where y_{t_1} = mean wet weight at the beginning of the month and y_{t_2} = mean wet weight at the beginning of the following month, was calculated for II+, III+, and IV+ perch sampled in the south basin each month from June to September during 1973 (Nakashima 1974). The three age-classes chosen represent fish between 83 and 200 mm fork length. Nakashima and Leggett (1975) have previously shown growth rates of perch in Lake Memphremagog to be stable from year to year.

We also used our data to develop estimates of daily ration based on methods previously employed by Keast and Welsh (1968) and Thorpe (1977). The Keast and Welsh method involves plotting the ratio of wet weight of stomach contents to wet body weight for each sample interval in the study period. Mean hourly rations at the observed troughs are subtracted from mean rations at peaks and these are then summed to estimate daily food consumption. We included empty stomachs in our analysis because our sampling intervals were short and we believe they represent normal variability in the data, not sampling error. Thorpe's method is much more complex and time-consuming than either the Keast and Welsh method or the method we derived and involves the calculation of evacuation rates (k) for each item consumed. The calculated k values are then employed to approximate the quantity of food consumed between collections. In our use of Thorpe's method we developed estimates of k for the contents of the entire stomach. These estimates were, furthermore, derived only from the slopes of the food weight/body weight curve following the evening peak of feeding. This was necessary because perch were observed to feed during the day and hence the slope of the postmorning peak may have been influenced by feeding, thus resulting in underestimates of the evacuation rate. Aside from these modifications, we followed the method of calculation described by Thorpe (1977).

Results

Diet Composition and Feeding Activity

Two trends were noted in the composition of the diet of the fish sampled. First, there were distinct seasonal differences in the diet within each of the three size-classes (Fig. 2). The greatest differences occurred between June and August, the period of highest feeding activity. In September and October, when feeding was suppressed, diets were more similar. The second trend was an increase in the diversity of items consumed as fish size increased (Fig. 2). Larger fish also tended to select larger food items such as fish and decapods.

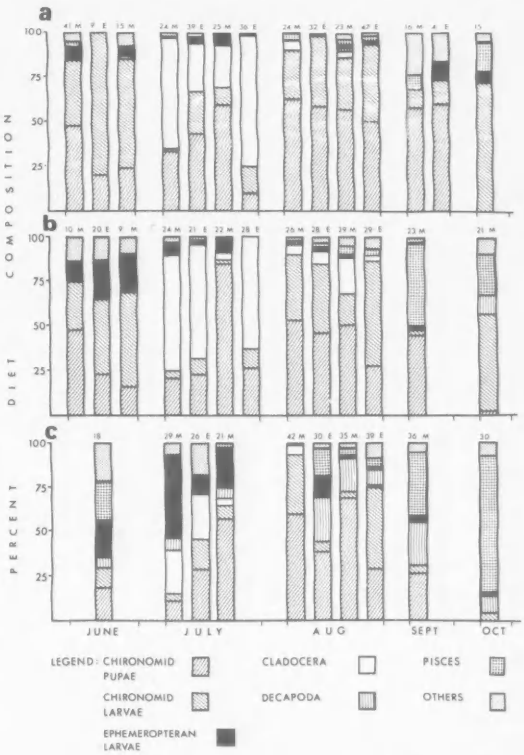

FIG. 2. Monthly diet composition of perch of different fork lengths: a, 83–105 mm; b, 151–200 mm; and c, 201–310 mm. Each bar represents a feeding peak; morning (M) and evening (E) peaks are separated when discernible. Sample sizes are given above each bar.

The composition of the diet during any one sampling period was more uniform. Perch <201 mm ate similar items during both morning and evening feeding periods, although considerable variation in the relative proportion of the dominant items in the diet at the daily feeding peaks (Fig. 2) did occur. In contrast, the larger perch (201–310 mm) constantly consumed different kinds and proportions of organisms between feeding peaks.

The feeding activity of perch was generally diurnal (Fig. 3) although this pattern was more evident in the smaller (83–150 mm) than the larger (201–310 mm) size-classes, the latter tending more towards a uniform pattern of feeding throughout both day and night. In addition, considerable day-to-day variation occurred. For example, the 151–200-mm size-class exhibited a distinct diurnal pattern of feeding in the first 24-h interval in August, whereas in the subsequent 24-h period only a single peak was evident (Fig. 3).

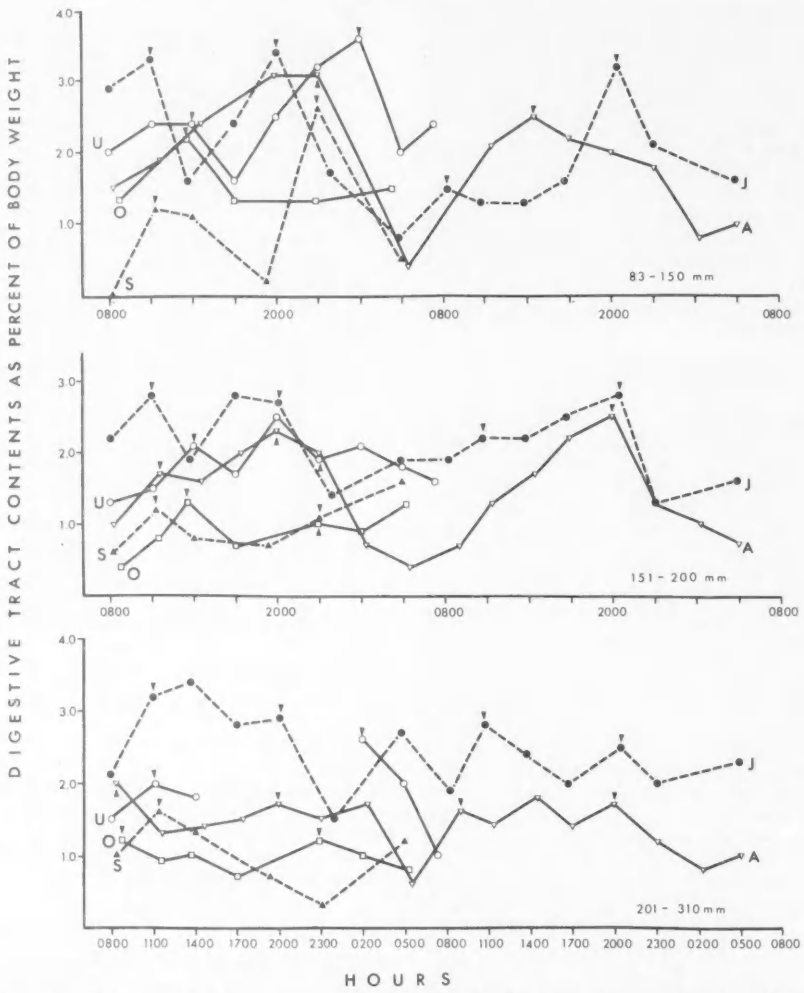

FIG. 3. Pattern of feeding activity determined for the three size-classes of perch in June (U), July (J), August (A), September (S), and October (O). Arrows (▼) indicate points used to calculate daily ration.

DAILY RATION

The daily ration of all three size-classes increased from June to July then decreased steadily to October (Table 1). Estimates of daily ration derived using the Keast and Welsh method (Table 1) were significantly less than those determined using our method or that of Thorpe (sign test: $n = 21$, $x = 0$, $P < 0.001$). Our method and that of Thorpe (1977), as modified by us (Table 1), give similar results with no clear pattern of difference between them (sign test: $n = 21$, $x = 10$, $P = 0.50$).

Discussion

The seasonal pattern in daily rations of yellow perch in the south basin of Lake Memphremagog, as estimated in this study, corresponds precisely with the seasonal growth pattern of the population (Fig. 4). This seasonal trend in feeding, and hence in growth, presumably results from the interacting effects of water temperature (as it affects metabolic rate), food availability, and gonad development. The method of Keast and Welsh (1968) and its derivatives (Fortin and Magnin 1972; Popova and Sytina 1977), which utilize serial sampling and force-feeding in order to incorporate evacuation rates, yield estimates of daily food consumption far below realistic levels. In our comparison, values based on this method were significantly less than those derived by the other two methods. Kitchell et al. (1977) simu-

TABLE 1. Estimates of daily ration for yellow perch (*Perca flavescens*) in the south basin of Lake Memphremagog derived using the method of Keast and Welsh (1968), the modified method of Thorpe (1977), and our method. Fish were placed into one of three divisions according to fork length (FL). July and August have two values, one for each 24-h period.

	FL, 83–150 mm			FL, 151–200 mm			FL, 201–310 mm		
	Keast and Welsh	This study	Modified Thorpe	Keast and Welsh	This study	Modified Thorpe	Keast and Welsh	This study	Modified Thorpe
June 1976	1.8	6.0	5.8	1.0	4.0	3.3	1.7	4.6	4.0[a]
July 1975	2.7	6.7	5.1	1.3	5.5	6.0	1.4	6.1	4.8
	1.2	4.7	4.1	2.0	5.0	5.5	1.5	5.3	4.7
Aug. 1975	1.6	3.1	5.5	1.3	4.0	3.4	1.6	3.7	5.5
	1.0	2.5	4.0	1.1	2.5	4.7	1.5	3.3	5.8
Sept. 1975	1.6	3.8	3.9	1.8	2.3	2.4	0.9	1.6	2.8
Oct. 1975	1.0	2.2	2.3	1.0	2.3	1.4	1.1	2.4	1.3

[a]Incomplete samples, i.e. two or more intervals when no fish were caught.

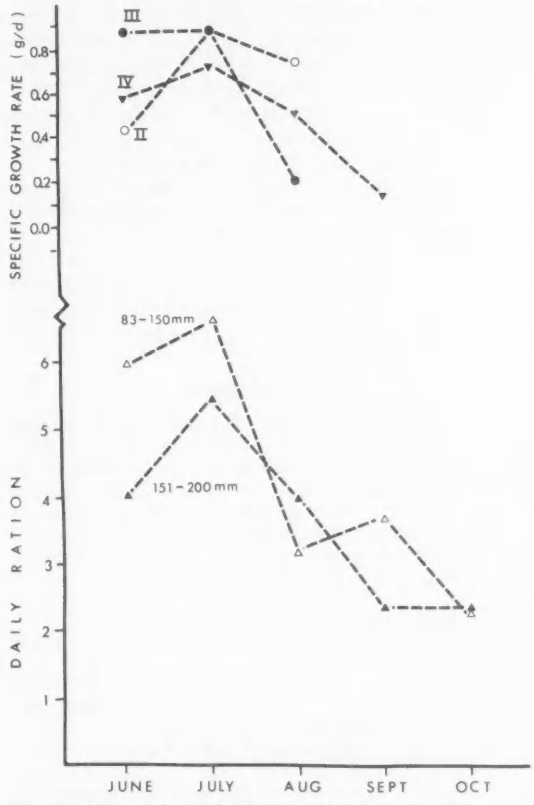

FIG. 4. Comparison of the seasonal pattern of daily ration (digestive tract contents as percent of body weight per day) of perch 83–200 mm with changes in specific growth rate of the II+, III+ and IV+ age-classes.

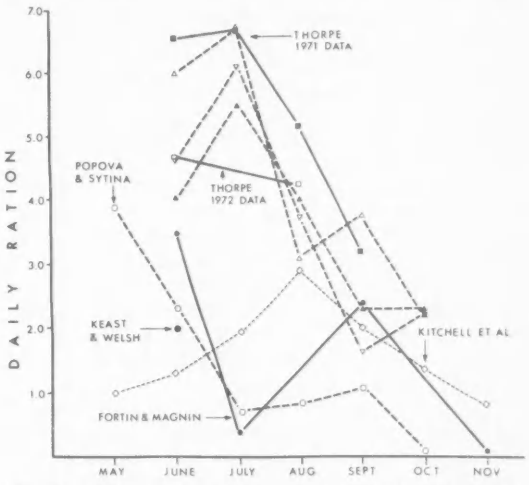

FIG. 5. Comparison of daily ration estimates (food consumed as percent of body weight per day) in this study [83–150 mm (▲ - - - ▲), 151–200 mm (△ - - - △), and 201–310 mm (▽ - - - ▽)] with values reported in the literature. Maintenance rations for a 10-g perch at monthly temperature equivalents as predicted by a bioenergetics model (Kitchell et al. 1977) (□ - - - □).

lated a series of growth–temperature–ration response curves for 10-g yellow perch based on data for *Perca fluviatilis* (Solomon and Brafield 1972) and *Stizostedion vitreum vitreum* (Kelso 1972; Swenson and Smith 1973). Their simulation indicates that maintenance rations vary from 0.9 to 3.4% for temperatures between 8 and 24°C (Fig. 5). Laboratory-derived estimates by Schneider (1973) corresponded with Kitchell et al.'s (1977) simulated values if body size and food type differences are considered. In general, estimates of daily ration derived from our data using the method of Keast and Welsh are below this maintenance level as are those independent estimates of perch daily ration reported by Keast and Welsh (1968), Fortin and Magnin (1972),

and Popova and Sytina (1977) (Fig. 5). This discrepancy occurred in spite of the fact that in the latter two studies an attempt was made to correct for evacuation of stomach contents. In contrast, our estimates, and those derived for adult *P. fluviatilis* in Loch Leven by Thorpe (1977), are above maintenance levels and, in general, the extent to which daily ration exceeds maintenance level on a seasonal basis is consistent with the observed pattern of growth (Fig. 5).

No evidence of a decline in relative ration levels with increasing fish size, as predicted by Ware's (1975) theoretical studies and suggested by Jezierska's (1974) laboratory studies on *P. fluviatilis*, was found (Table 1). This may result from the lack of precision still inherent in in situ estimates.

There appears to be little difference in the estimates derived by the method we described and that of Thorpe, in spite of the greater sophistication of the latter which renders it too time-consuming for regular in situ use. The variation in estimates determined from the two methods derives, in part, from the validity of the assumptions in the methods as they relate to conditions at the time of sampling. Both methods assume a synchrony in feeding. Failure to meet this assumption affects the Thorpe (1977) method more directly because of its influence on the calculation of evacuation rates. His method also assumes linearity of food consumption between samplings. Thorpe (1977) suggested the considerable variation between his 1971 and 1972 estimates of daily ration (Fig. 5) may have resulted from annual differences in diet between the years. Our 48-h samples indicate, however, that differences of similar magnitude may occur from day to day. This inherent variability may negate some of the potential advantages of the greater rigor of his method.

Our method uses the contents of both the intestine and stomach rather than the traditional approach of the stomach contents alone. Two assumptions are implied. First, the food from the previous feeding period has cleared the digestive tract. Secondly, there is negligible absorption of matter via the intestine during the active feeding period when the fish are caught.

If food were to remain from a previous feeding period, the method would overestimate actual ration by including the weight of some matter twice. Evacuation rates calculated in laboratory circumstances are not applicable to the field (Thorpe 1977). Further, Thorpe demonstrated that serial sampling of captured fish denied access to food underestimated actual digestion rates. He concluded that evacuation rates had to be determined from the fish captured at periodic intervals. Because our method and the modified version of Thorpe give essentially similar results, we conclude that the evacuation rates in the field were sufficient to allow gut clearance between feeding peaks.

If matter is absorbed via the intestine, this would result in an underestimate of the actual amount of food consumed. We suggest that during synchronous feeding the majority of food in the stomach and anterior portion of the intestine is unprocessed. Our observations indicate that much of the food in the stomach has not been subjected to the process of mechanical and chemical breakdown and therefore no absorption would have taken place. However, we concede that some matter may have been absorbed in the intestine but at present there is no way to determine how much. If we were able to employ a correction factor, our determinations of daily ration would be revised upwards.

Despite the main assumptions of complete digestive tract clearance between feeding peaks and negligible absorption of matter in the intestine during peak feeding periods, our method provides estimates comparable to a modification of Thorpe's (1977) method which is rigorous and does account for these two assumptions. Therefore we conclude that their influence on the final calculations are minimal.

The results of this study strongly suggest that our method, which eliminates the need to laboriously identify all items in the diet and to calculate evacuation rates for each item, yields estimates that do not differ materially from those derived from the more complex method of Thorpe (1977). Because of this similarity in precision, and the greater ease of calculating daily food consumption with our method, we recommend its use for field determination of daily ration levels. To achieve greater accuracy in in situ estimates of daily ration, a much greater understanding of the feeding chronology of fish must be obtained. Our findings indicate that this will require a much more complete series of feeding studies employing short sampling intervals and continuing at least 48 h and preferably longer.

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Origin of Deposited Material Sedimented in a Marine Bay[1]

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HARGRAVE, B. T., AND S. TAGUCHI. 1978. Origin of deposited material sedimented in a marine bay. *J. Fish. Res. Board Can. 35: 1604–1613.*

Suspended and sedimented particulate carbon, nitrogen, chlorophyll *a*, and phaeophytin were measured at various depths throughout the year in a small marine bay. Seasonal and vertical differences in sedimentation rates were not simply related to changes in concentration of suspended particulate matter. Chlorophyll *a*/total pigment, carbon/nitrogen, and carbon/chlorophyll *a* ratios in suspended and sedimented material were usually different. Sedimentation rates generally increased with depth with greatest increases during periods of low stratification. Resuspension and horizontal transport of sedimenting material was implied by discontinuities in sedimentation at particular depths. Annual sedimentation of particulate carbon at 20 m depth (below the seasonal thermocline) was equivalent to 15% of the estimated supply from photosynthetic and chemosynthetic production, river discharge, and sewage input. Material deposited during periods of stratification, however, which coincided with high rates of primary production and increased zooplankton biomass during the summer, contained high amounts of carbon and chlorophyll *a* with a low carbon/nitrogen ratio indicative of a supply from biological production. Thus, although a small fraction of the total suspended particulate matter annually available was deposited, large differences in the quantity and quality of sedimented material occurred seasonally.

Key words: sedimentation, resuspension, suspended particulate matter, biological production, organic supply, coastal embayment

HARGRAVE, B. T., AND S. TAGUCHI. 1978. Origin of deposited material sedimented in a marine bay. *J. Fish. Res. Board Can. 35: 1604–1613.*

Nous avons mesuré à diverses profondeurs, durant toute l'année, dans une petite baie de mer, le carbone particulaire en suspension ou déposé, l'azote, la chlorophylle *a* et la phéophytine. Il n'y a pas de relation simple entre les différences verticales et saisonnières des taux de sédimentation et des changements dans la concentration des matières particulaires en suspension. Les rapports chlorophylle *a*/pigment total, carbone/azote et carbone/chlorophylle *a* dans le matériel en suspension et déposé sont ordinairement différents. Les taux de sédimentation augmentent généralement en fonction de la profondeur, les plus fortes augmentations se produisant durant les périodes de faible stratification. Des discontinuités dans la sédimentation à des profondeurs particulières nous font croire qu'il y a resuspension et transport horizontal des matières en voie de sédimentation. La sédimentation annuelle du carbone particulaire à 20 m de profondeur (en dessous de la thermocline saisonnière) équivaut à 15% de la production estimée par photosynthèse ou chimiosynthèse, le débit des rivières et l'apport d'égouts. Cependant, les matières déposées durant les périodes de stratification qui coïncident avec les taux élevés de production primaire et biomasse zooplanctonique accrue en été, contiennent de grandes quantités de carbone et de chlorophylle *a* avec faible rapport carbone/azote, signe d'un apport provenant de la production biologique. Ainsi, bien qu'une petite fraction des matières particulaires totales en suspension disponibles annuellement soit déposée, il se produit saisonnièrement de grandes différences dans la quantité et la qualité des matériaux déposés.

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SEDIMENTATION removes suspended material from the water column. It also provides input of energy and materials to bottom communities and thus links production in the water column with that at the sediment surface. Measurements of sedimentation by suspending collectors at fixed depths in the water column have usually been intended to measure nutrient input to sediments. While some studies have quantitatively related sedimentation to suspended material potentially available for deposition, comparisons have yielded conflicting results. Toyoda et al. (1968), Steele and Baird (1972), and Ansell (1974) observed no relation while others (Hutchinson 1938; Riley 1965; Vollenweider 1966; Nakajima and Nishizawa 1972; Rigler 1973; Boyce 1974; Kimmel and Goldman 1977) have either inferred or observed a close relation between suspended and sedimented concentrations of particulate matter.

In this study we compare seasonal changes in sedimentation rate and concentration of suspended material at various depths in Bedford Basin, a small enriched embayment in Nova Scotia (Platt and Conover 1971; Platt and Filion 1973; Platt 1975; Taguchi et al. 1975). Differences in sedimentation with depth and seasonal changes in carbon, nitrogen, and plant pigment concentration in suspended and deposited material show that suspended material does not sediment directly. Sedimentation is compared with particulate carbon supply from phytoplankton production, chemosynthesis, river discharge, and sewage input to quantify the magnitude of sedimentation as a pathway for removal of suspended particulate matter.

Materials and Methods

Sampling was carried out from October 1973 to November 1974 at a central station (70 m maximum depth) in Bedford Basin (see Platt and Conover 1971). The bay (17 km^2) lies at the landward end of a coastal embayment which forms Halifax Harbour. Bedford Basin joins the harbor through a narrow channel which contains a sill at 15 m depth. Thermoclines and haloclines form at or above this depth in the Basin to create an upper layer subject to tidal flushing and a lower layer with limited exchange. Alternating periods of stratification and mixing (when exchange of water occurs across the sill), however, ensure that deep water in the Basin is periodically renewed (Platt et al. 1970). Data illustrating seasonal changes in stratification (June–September) and periodic renewal of deep water are presented by Hargrave et al. (1976).

Water samples for determination of suspended particulate matter, collected at 0930 h at 0, 2.5, 5, 10, 15, 20, 30, 40, and 60 m with a 6-L PVC Van Dorn bottle, were filtered immediately through nytex mesh (153 μm) and stored in dim light for 2 h. One-litre subsamples were filtered through GFC filters which were then extracted for chlorophyll *a* and phaeophytin following the method of Yentsch and Menzel (1963) modified by Holm-Hansen et al. (1965). Other one-litre subsamples were filtered through preashed silver filters (Flotronics 0.8 μm) which were dried at 60°C. A Hewlett Packard F&M 185 CHN analyzer was used to measure particulate carbon and nitrogen. The coefficient of variation of 10 replicate standard samples up to 2 mg dry weight was 2%. The standard deviation of duplicate determinations of carbon and nitrogen in subsamples from one water sample amounted to 10% of mean values. Previous studies in Bedford Basin have quantified spatial and temporal variation in phytoplankton production, chlorophyll, and zooplankton biomass (Platt and Conover 1971; Platt and Filion 1973). Short-term variance in these parameters is small compared with seasonal differences (Platt 1975; Taguchi et al. 1975). Thus, no attempt was made to correct for horizontal or diel variation in suspended particulate concentrations measured in this study.

Water samples for temperature, salinity, and suspended particulate matter determinations were collected with Nansen reversing bottles at the same depths. Particulate and dissolved organic carbon entering Bedford Basin through the Sackville River were determined on unfiltered and filtered (0.8-μm preashed Flotronics silver filters) samples collected twice monthly throughout the year at the river mouth. Sample volumes of 40 μL were injected and combusted at 950°C in a Beckman (model 195) infrared CO_2 analyzer.

Sediment traps consisted of PVC cylinders (7.5 × 31 cm) closed at one end and held in stainless steel holders (described by Webster et al. 1975). Four cylinders were mounted in each holder. Four of these arrays were clamped at 20, 30, 40, and 60 m along a stainless steel wire held in position by an anchor and subsurface float suspended at 8 m. A surface float and radar reflector was tethered to the subsurface buoy for retrieval.

Traps were initially suspended at 20 m (June 18–July 22, 1972) at three different locations around the central sampling site. An average of 1.45 g dry weight $\cdot m^{-2} \cdot day^{-1}$ was collected in the 12 cylinders with a coefficient of variation (σ/mean) of 0.16. Variation between four cylinders at each location ranged from 0.08 to 0.23. Since differences in total weight sedimented at one site were comparable to differences at three sites, sedimentation was measured at a single station. Traps were emptied, cleaned, and replaced approximately every 28 d over 380 d. Details of analyses for total dry weight, organic matter, plant pigments, and microscopic examination of sedimented material are given in Hargrave et al. (1976).

The effect of sediment trap design on collection efficiency or degradation of deposited material was not considered. Kirchner (1975) observed that cylinders were preferable to funnel-shaped collectors and visual examination of sediment deposited in glass cylinders exposed in Bedford Basin showed that no resuspension occurred during trap retrieval. Plant pigments and organic matter were likely degraded between collection intervals and sedimented material may be considered best as the supply of relatively stable organic matter residual after bacterial attack. Zooplankton fecal pellets with intact peritrophic membranes were collected at all depths, indicating either that bacterial decomposition (as observed by Ferrante and Parker 1977) had not occurred or that feces were produced at all depths in the water column.

Results and Discussion

COMPARISON OF SUSPENDED AND SEDIMENTED PARTICULATE MATTER

Individual seasonal patterns of deposition of particulate carbon, nitrogen, chlorophyll *a*, and phaeophytin

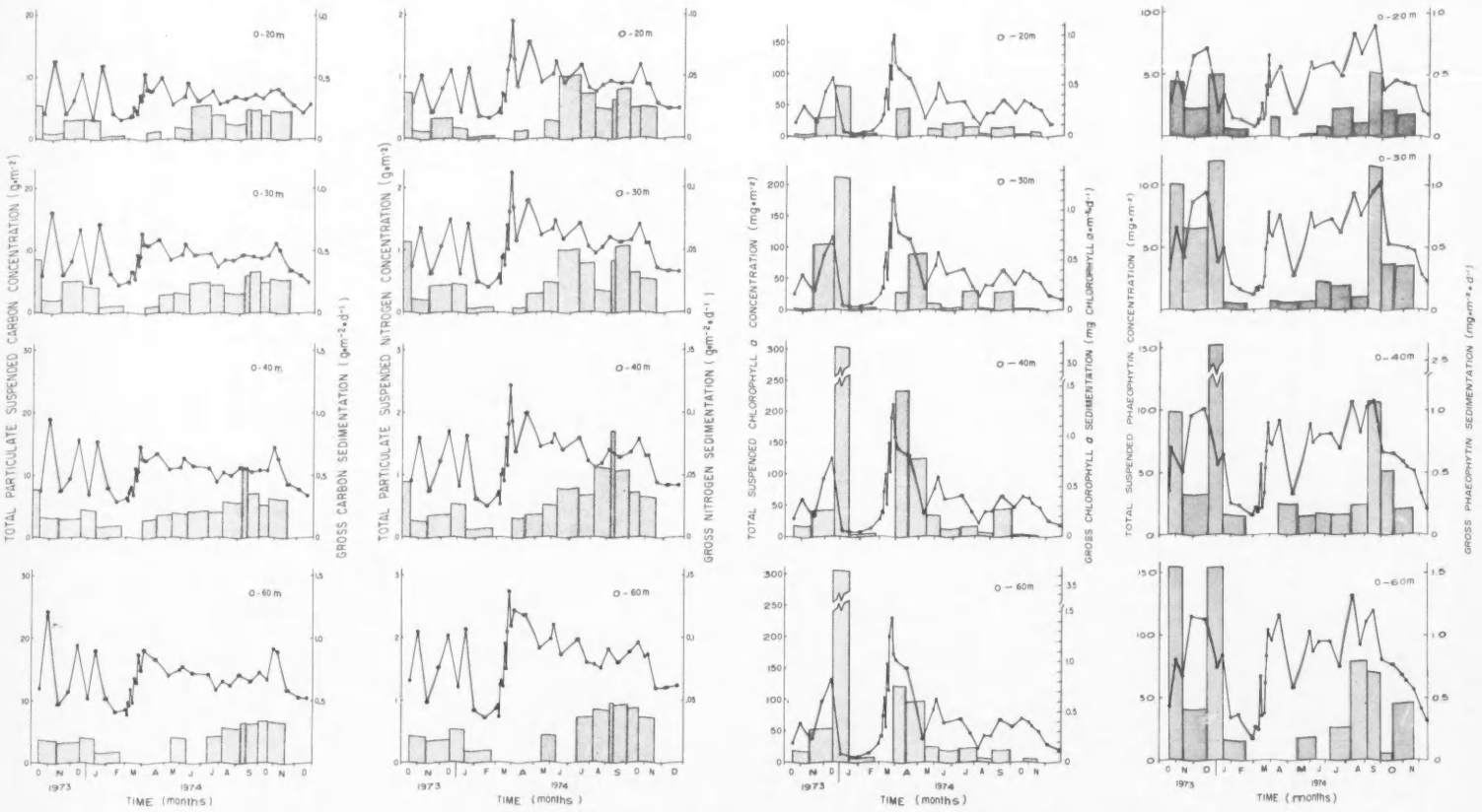
0 - 20 m
0 - 30 m
0 - 40 m
0 - 60 m
TOTAL PARTICULATE SUSPENDED CARBON CONCENTRATION (g·m⁻²)
GROSS CARBON SEDIMENTATION (g·m⁻²·d⁻¹)
TOTAL PARTICULATE SUSPENDED NITROGEN CONCENTRATION (g·m⁻²)
GROSS NITROGEN SEDIMENTATION (g·m⁻²·d⁻¹)
TOTAL SUSPENDED CHLOROPHYLL a CONCENTRATION (mg·m⁻²)
GROSS CHLOROPHYLL a SEDIMENTATION (mg CHLOROPHYLL a·m⁻²·d⁻¹)
TOTAL SUSPENDED PHAEOPHYTIN CONCENTRATION (mg·m⁻²)
GROSS PHAEOPHYTIN SEDIMENTATION (mg·m⁻²·d⁻¹)
O N D J F M A M J J A S O N D
1973
1974
TIME (months)

FIG. 1. Sedimentation (histogram) and integrated suspended concentration of particulate carbon, nitrogen, chlorophyll *a*, and phaeophytin at different depths in Bedford Basin during 1973 and 1974.

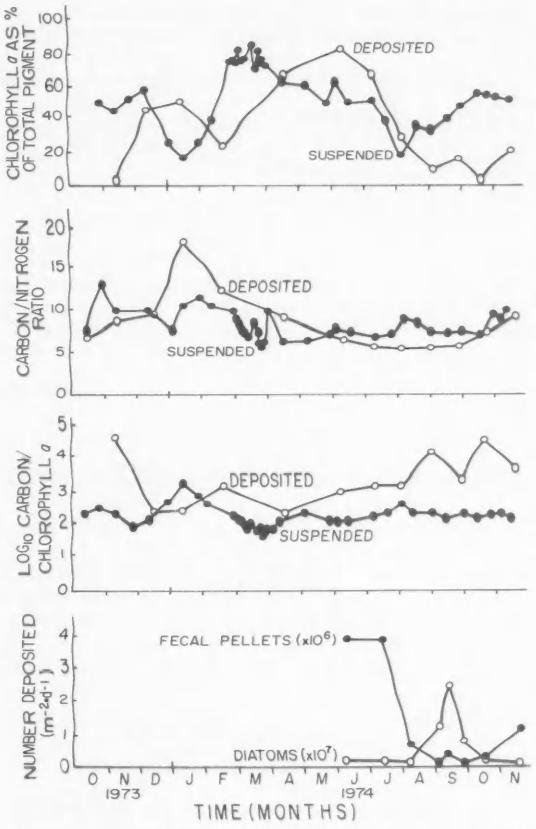

FIG. 2. Comparison of chlorophyll *a* as a percent of total pigment and of carbon/nitrogen and carbon/chlorophyll *a* ratios in suspended and deposited particulate matter and numbers of fecal pellets and diatom frustules deposited at 20 m in Bedford Basin.

were similar at various depths (Fig. 1). Seasonal peaks in sedimentation of the four substances, however, were not similar. No large changes in carbon and nitrogen sedimentation occurred during December–January, a period of maximum plant pigment deposition. Also, sedimentation of chlorophyll *a* and phaeophytin increased greatly with increased depth during fall and winter while carbon and nitrogen did not show similarly large increases. These seasonal- and depth-related changes were not clearly paralleled by changes in suspended concentration. Carbon and nitrogen sedimentation, between successive collection periods, for example, often differed significantly with no corresponding change in suspended concentrations. Increased chlorophyll *a* concentration during November 1973 and March–April 1974 was not reflected immediately in increased sedimentation, but was apparent in subsequent collection periods.

The lack of a consistent relationship between suspended and sedimented particulate matter at various depths is also evident in differences in chlorophyll *a*, measured as percent of total pigment, carbon/nitrogen ratios, and carbon/chlorophyll ratios in suspended and sedimented material measured throughout the year (Fig. 2). There were often significant differences in these measures in material sedimented over consecutive depth intervals which were not reflected in suspended material present at that time (Hargrave et al. 1976; Fig. 1). In addition, high rates of fecal pellet deposition at 20 m between June and mid-July (Fig. 2) occurred when few pellets were observed suspended in the water column, yet these were numerous above 20 m depth during late April and early May (Taguchi unpublished data). Similarly, high proportions of chlorophyll *a* as percent of total pigment occurred in suspended material during March and April while similar values occurred in material deposited during May and June.

The observations imply that not all suspended material is deposited at equivalent rates or, equally probable, that there are prolonged and variable time lags before deposition, which depend on the origin of particulate matter. Decomposition of sediments in traps could also change the organic content and make comparison with suspended matter misleading. Also, sedimentation measurements are integrative over time while samples of suspended material are discrete in space and time.

Despite these problems of interpretation, it is apparent that the bulk of deposited material is not simply derived by sedimentation of a constant fraction of particulate matter suspended in the water column. Thus, while carbon/nitrogen and carbon/chlorophyll *a* ratios in sedimented material tended to decrease and increase, respectively, between April and September, values for these ratios in suspended matter did not change in a similar way (Fig. 2). Even the abundance of zooplankton fecal pellets, which made up the bulk of settled material (>50% on a volume basis) during June, was not apparent in changes of values for these ratios.

Another interpretation of these data is to conclude that carbon/chlorophyll *a* and carbon/nitrogen ratios are not particularly sensitive indicators for seasonal changes in the nature of deposited particulate material. However, changes in these ratios during the disappearance of stratification in September and October did occur when zooplankton fecal pellets were deposited in reduced numbers and sedimentation of diatoms (*Skeletonema costatum*) with intact chloroplasts increased by two orders of magnitude (Fig. 2). Only carbon/nitrogen ratios in suspended and deposited material were similar during this period.

DEPTH-RELATED DIFFERENCES IN SEDIMENTATION

Depth-dependent increases in sedimentation of particulate carbon, nitrogen, chlorophyll *a*, and phaeophytin are clearly shown by estimates of annual total deposi-

TABLE 1. Annual sedimentation[a] ($g \cdot m^{-2} \cdot yr^{-1}$) of organic carbon, nitrogen, chlorophyll *a*, and phaeophytin at various depths in Bedford Basin.

Depth (m)	20	30	40	60	Percent increase[b]
Carbon	55.1	66.0	75.9	75.7	37.4
Nitrogen	7.6	8.7	10.6	9.4	23.7
Chlorophyll *a*	.056	.116	.230	.183	226.8
Phaeophytin	.076	.149	.193	.203	167.1

[a]Measurements of sedimentation were not obtained at some depths during the year because of accidental loss of sediment traps (Fig. 1). Deposition rates were interpolated between depths or sampling dates in these instances to provide annual estimates. Values for sedimentation during March 1973 (Hargrave et al. 1976) were substituted for data not obtained during March 1974.

[b]Increase in sedimentation between 20 and 60 m expressed as a percent of that at 20 m.

tion at specific depths (Table 1). Annual sedimentation at 60 m was higher than that at 20 m for all four substances but the magnitude of increase was not similar. Deposition of particulate nitrogen was the least affected by depth, while vertical differences in chlorophyll sedimentation were large with a particular anomally at 40 m during April where high rates of deposition did not occur at shallower or deeper depths (Fig. 1).

Comparison of sedimentation at 20 and 60 m on a seasonal basis was used to consider factors that might control deposition. If sedimentation at both depths was similar (ratio of 20:60 = 1.0) it might be assumed that material (such as inorganic particles or fecal pellets) settled only vertically with a high sinking rate. Input at 20 m would equal sedimentation at 60 m with no significant loss or gain, or a balance between removal and supply, over intervening depths. Ratios <1 would result if material was transported by horizontal advection at particular depths or added by production or resuspension at intervening depths within the water column. Values >1 would indicate loss of material by degradation or consumption. Although simplistic, the comparison provides a useful measure of similarity in rates of deposition over depth which is independent of absolute sedimentation rates.

Since annual sedimentation of all substances increased with depth (Table 1), the ratio of sedimentation at 20:60 m throughout the year was usually <1 (Fig. 3). During late winter and spring, carbon and chlorophyll *a* sedimentation at 20 m was between 30 and 50% of that at 60 m. This also was the period of minimum density gradient ($>2\sigma_t$ units) in the water column between 0 and 60 m. During December and July, however, when a high density gradient existed in the water column, the ratio of sedimentation at 20:60 m approached or exceeded 1. During autumn, when vertical density differences were minimized through cooling and mixing, carbon sedimentation at 60 m again ex-

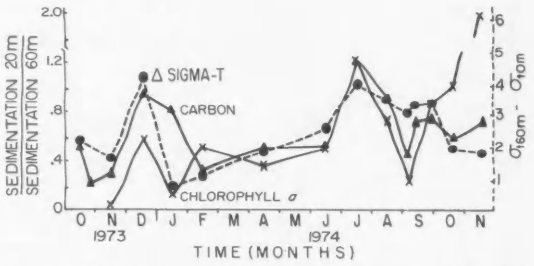

FIG. 3. Seasonal changes in the ratio of carbon and chlorophyll *a* sedimentation at 20 and 60 m and the difference in *sigma-t* between 0 and 60 m. Periods of stratification correspond to increases in the difference in σ_t between 0 and 60 m.

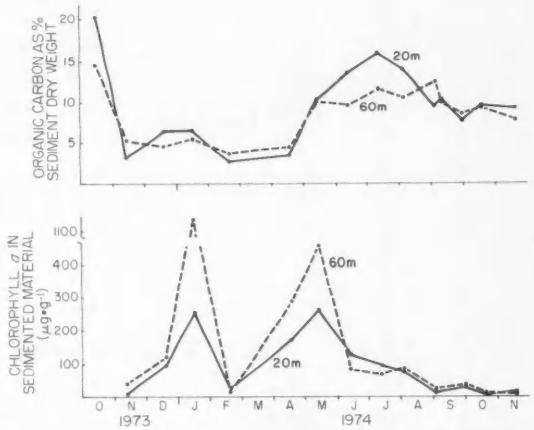

FIG. 4. Seasonal changes in particulate organic carbon and chlorophyll *a* in material deposited at 20 and 60 m in Bedford Basin.

ceeded that at 20 m by approximately 30% but chlorophyll *a* sedimentation at 20 m remained high relative to that measured in deeper water. Excessive deposition at 60 m over that at 20 m thus occurred during periods of low stratification. Resuspension and physical transport (both horizontal and vertical) could both increase sedimentation with depth at these times.

Comparisons of organic content of material sedimented at various depths also show that depth-related changes in sedimentation were at least partially related to differences in organic content. For example, significant decreases in organic carbon (and nitrogen) occurred in material settled at different depths during summer stratification (Fig. 4; Hargrave et al. 1976). While chlorophyll *a* in material collected at 20 and 60 m was similar during this period, significant increases occurred at 60 m during January and May. This provides additional evidence that factors that cause increased deposition of particulate matter with increasing depth (Table 1) do not affect plant pigments and organic

TABLE 2. Index of determination (values of r^2) derived from linear regression analyses comparing sedimentation at different depths in Bedford Basin (data in Fig. 1).

	Depth (m)	30	40	60
Carbon	20	.81	.47	.53
	30		.55	.73
	40			.64
Nitrogen	20	.83	.53	.62
	30		.43	.70
	40			.59
Chlorophyll *a*	20	.88	.90	.89
	30		.74	.84
	40			.94
Phaeophytin	20	.86	.69	.63
	30		.70	.58
	40			.63

carbon (and nitrogen) to the same degree or even simultaneously.

The extent to which sedimentation differs vertically in a water column can also be assessed by measuring coherence between sedimentation rates at various depths. Seasonal data were combined to calculate a matrix of linear correlation coefficients on this basis (Table 2). Sedimentation at 20 m was always closely related to that at 30 m with similar correlation coefficients for all four substances. With the exception of those for chlorophyll *a*, however, coefficients between all other depths were significant but considerably lower with no depth-dependent trend. Deposition of chlorophyll *a* was highly correlated between all depths, indicating that sedimentation at any given time during the year was similar throughout the water column. Thus, as observed above, horizontal and vertical processes of supply which transport particulate matter to various depths below 20 m in Bedford Basin do not affect chlorophyll and other measures of organic content in similar ways.

Seasonal Supply of Deposited Material

Comparison of changes in phytoplankton primary production, zooplankton biomass, and river discharge indicates seasonality in s pplies of organic matter in Bedford Basin to which differences in the amount and nature of sedimented material might be related (Fig. 5). For example, minimum carbon/nitrogen ratios in material deposited during stratification (Fig. 2) corresponded to a predominance of fecal pellets or diatoms in settled particulate matter. Chlorophyll *a* content in sedimented material also decreased continuously during this time, indicating that pigment degradation products increased in relative concentration from a minimum during June to a maximum during October.

High rates of chlorophyll *a* and phaeophytin sedimentation and increased chlorophyll *a* in sedimented material also occurred during December and January,

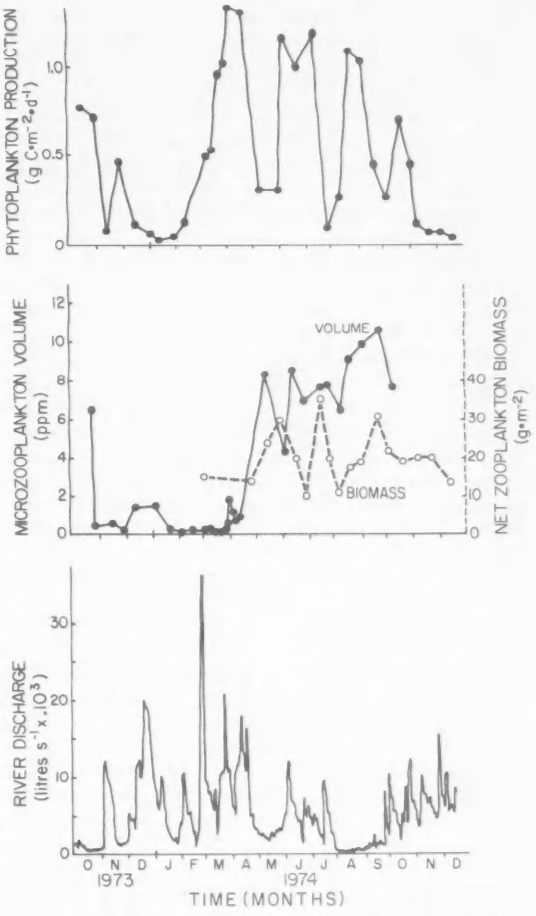

FIG. 5. Comparison of annual changes in phytoplankton primary production (from Taguchi and Platt 1977), microzooplankton volume (0–20 m) (Taguchi unpublished data), net zooplankton biomass (from Sameoto 1971), and discharge from the Sackville River measured in Bedford Basin during 1973 and 1974.

when the carbon/nitrogen ratio in settled materials was maximum (Fig. 1 and 2). This could have been associated with a bloom of the dinoflagellate *Ceratium* during October and November 1973. Increased concentrations of plant pigments, reduced carbon/chlorophyll *a* ratio in suspended material and a peak in primary production coincided with the presence of *Ceratium* (Fig. 2 and 5; Taguchi *et al.* 1975). Since these cells were not ingested by zooplankton (Taguchi unpublished observations), it is likely that after a 2–3-wk delay sedimentation of intact cells occurred without incorporation in fecal pellets.

The Sackville River which enters Bedford Basin has a minimum discharge during the summer months when

TABLE 3. Seasonal average values for water discharge[a] and organic carbon in water entering Bedford Basin from the Sackville River during 1973 and 1974. n = number of observations for measurement of organic carbon.

Period	Total river discharge ($m^3 \cdot 10^6$)	n	Organic carbon	
			Particulate ($mg \cdot L^{-1}$)	Dissolved ($mg \cdot L^{-1}$)
1973				
Nov. 1–30	10.4	4	0.8	13.5
Dec. 1–31	24.1	4	1.6	12.2
1974				
Jan. 1–Feb. 28	31.0	3	0.8	8.4
Mar. 1–May 31	56.2	3	1.2	11.9
June 1–Aug. 31	18.1	3	4.3	7.4
Sept. 1–Oct. 31	22.6	5	0.8	10.6
Total	162.4	$\bar{x}$	1.6	10.7

[a]Data provided by Water Survey of Canada, Water Management Division, Halifax, from a continuously recording gauge.

sedimentation of particulate carbon and nitrogen is maximum (Fig. 1 and 5). Discharge during December, however, is the highest per month for the entire year (Table 3), and this may contribute particulate matter typified by carbon/nitrogen ratios greater than 15 (Fig. 2). Such high ratios were observed only in material trapped at 20 m during January. Thus, particulate matter entering the Basin from the river either settles at depths shallower than 20 m (as in the vicinity of the river mouth) or it is removed by tidal flushing of the stratified surface layers formed during excessive runoff.

Comparison of Sedimentation with Other Processes of Carbon Supply and Loss

A comparison of annual rates of particulate matter supply and loss in a water body is useful for equating the magnitude of processes that add and remove materials. Carbon provides a common basis for comparing rates of input or removal that have either been measured or can be calculated for Bedford Basin. Even though several processes have not been quantified (for example, atmospheric fallout, land runoff, respiratory oxidation of suspended material) or accurately estimated throughout the year (tidal export and import, sewage input), sedimentation appears to represent a significant pathway of particulate organic carbon flux at 20 m depth (Table 4). Input of dissolved organic carbon from the Sackville River is included as a particulate supply since precipitation and flocculation of filter passing (dissolved) material could occur. Also, both dissolved and particulate organic carbon from this source are assumed to be evenly distributed over the Basin surface, yet high rates of deposition are known to occur in the vicinity of the river mouth. Since this occurs, sedimentation is a larger fraction of the total supply at the central Basin site than the calculations indicate.

TABLE 4. Annual supply and loss of organic carbon in the upper 20 m of Bedford Basin.[a] Values in parentheses were not measured.

	$g\,C \cdot m^{-2} \cdot yr^{-1}$	Percent of annual total
Supply		
Photosynthetic production[b]	200 ± 10	55
Chemosynthetic production[b]	40 ± 7	11
River discharge[c]		
dissolved	102	28
particulate	15	4
Sewage input[d]	(7)	2
Total	364	
Loss		
Sedimentation[c]	55	15
Export[e]	(211)	58
Respiration[f]	(98)	27

[a]Calculated on a square-metre basis for the surface area of the Basin (17 km^2) for the volume present above the 20-m depth contour (240×10^6 m^3).

[b]Taguchi and Platt (1977). Primary production is restricted to the upper 20 m while 80% of dark $^{14}CO_2$ fixation for the total water column occurs to this depth.

[c]Measured (Tables 1 and 3).

[d]Calculated for the estimated population of 30 000 with high-rate secondary treatment (52.5 g dry organic matter·person^{-1}·d^{-1}, 50% organic carbon, sewage treatment 60% effective).

[e]58% of production exported over 24 h, Platt and Conover (1971), assumed to apply to all sources of organic carbon entering the basin above 20 m.

[f]Calculated by difference.

The 37% increase in annual particulate carbon sedimentation between 20 and 60 m (Table 1) is equivalent to the addition of $21\,g\,C \cdot m^{-2} \cdot yr^{-1}$. Significant photosynthetic production seldom occurs below 20 m in Bedford Basin but approximately 20% of annual dark assimilation of $^{14}CO_2$ ($10\,g\,C \cdot m^{-2}$) occurs between 20 and 60 m (Taguchi and Platt 1977). Advective transport of suspended material by tidal exchange might also intermittently add (and remove) material below 20 m. Strong gradients exist in temperature, salinity, and nutrient concentrations due to the presence of a sill across the entrance channel at this depth (Platt et al. 1970). This implies that suspended material below 20 m is not subject to tidal exchange. Incursions of deep water do occur, however, between alternating periods of stratification and mixing (Hargrave et al. 1976). Import of suspended particulate matter would also occur during these mixing events. In addition, resuspension of previously settled material, particularly during periods of low stratification, or production of fecal material by vertically migrating zooplankton could contribute to sedimented particulate matter at specific depths in deep water.

General Discussion

Zooplankton feces, which predominate in sedimented material deposited in some marine coastal areas (Steele and Baird 1972; Seki et al. 1974), were quantitatively important in material deposited in Bedford Basin during summer when the water column was most stratified (Fig. 2). When low vertical density gradients occurred (during periods of vertical mixing in December and September), however, *Ceratium* and *Skeletonema* cells with intact chloroplasts were also deposited in large numbers. Throughout the remainder of the year, even during the spring bloom, the bulk of material deposited in Bedford Basin was amphorous debris as particles and flakes. These seasonal differences and discontinuities between sedimentation at 20 and 60 m during periods when vertical density gradients were least (Fig. 3) show that seasonal and depth-dependent changes in absolute rates of sedimentation are determined by water column physical structure as well as by the nature of the deposited material.

Our observations (Table 1) and those in previous studies in shallow water environments (Moore 1931; Toyoda et al. 1968; Steele and Baird 1972; Pennington 1974; Ansell 1974; Oviatt and Nixon 1975; Webster et al. 1975; and Davies 1975) show that the quantity of material trapped generally increases with depth. Vertical profiles of sedimentation, however, also show anomalies at particular depths (Steele and Baird 1972; Davies 1975). Differences were usually not due to differences in total weight of material trapped, as might be expected if turbulence affected sediment collection at particular depths or if physical loss occurred on trap retrieval. If any changes in sedimentation with depth were to occur, decreases might be expected due to degradation and consumption during sinking. However, resuspension of bottom sediments at various depths and subsequent horizontal transport, in situ autotrophic and heterotrophic production, fecal pellet production by migrating animals, and intrusions of water at depth could account for the observations.

In our study, total weight sedimented generally increased with depth, but samples at some depths contained significantly different organic or pigment content compared to those collected during the same period at other depths. Large differences in fecal pellet and phytoplankton cell numbers also occurred in these samples (Hargrave et al. 1976). Blooms of heterotrophic organisms that occurred at specific depths (Taguchi and Platt 1977) or fecal pellets produced by *Sagitta elegans* which is abundant in deep water from May to October in Bedford Basin (Sameoto 1973) could have contributed material to discrete depth layers. In any case, material must either have been transported horizontally or produced between sampling depths. It could not have settled vertically. These differences make correction for resuspension impossible, as suggested by Gasith (1975), since the origin of settled material at a specific depth is unknown.

Seasonal changes in organic and pigment content of suspended and deposited material (Fig. 2) also indicate that sedimentation is not directly linked to suspended material in Bedford Basin. Increased chlorophyll *a* sedimentation during late December and early April followed blooms of phytoplankton at the surface with delays of 2–3 wk (Fig. 1 and 5). Zooplankton were not abundant during these periods and algal cell deposition must have occurred following the period of maximum growth. Lund et al. (1963) observed that after active cell growth ceased, loss per unit population of *Asterionella* in Lake Windermere increased fivefold while density stratification remained unchanged. Stephens et al. (1967) also noted increased sedimentation of material with a high pigment content and a C/N ratio comparable to living phytoplankton 2 mo after the spring phytoplankton bloom in a coastal bay. Delayed sedimentation was not directly related to the deepening of the euphotic zone and it was thought to be independent of zooplankton grazing.

In contrast to these observations, previous studies of primary production and sedimentation in several lakes have shown a close seasonal relation between particulate matter supply and deposition (Wetzel et al. 1972; Rigler 1973; Bloesch et al. 1977; Kimmel and Goldman 1977). Although vertical differences in sedimentation were observed in some of these studies, when additional particulate matter sedimented with increasing depth, the increase was not large nor were there great differences in the organic composition of material deposited at different depths. The lack of large vertical discontinuities in sedimentation, also absent in our study during July (Fig. 3), shows that direct vertical sinking of particulate matter can occur presumably when water motion is minimal and when the settling velocity of particles is increased.

Processes that add material to increase sedimentation with depth in Bedford Basin, whether physical or biological, do not affect organic carbon, nitrogen, and plant pigments similarly (Tables 1 and 2). Increased plant pigment deposition during the winter and in April, for example, was maximum at 40 m (Fig. 1), even though chlorophyll *a* could only have originated above 20 m depth (Taguchi and Platt 1977). Horizontal transport and sedimentation of previously settled phytoplankton must have occurred at this depth. No extensive macrophyte communities presently exist in Bedford Basin and thus a seasonal supply of organic matter from this source, as occurs in St. Margaret's Bay (Webster et al. 1975), does not occur. Excessive sedimentation of chlorophyll *a* with depth is surprising since degradation of the pigment after cell death is known to be rapid. Little undegraded pigment usually exists suspended in the water column below the euphotic zone in Bedford Basin (Platt and Conover 1971; Taguchi et al. 1975) and integrated concentrations over depth in our study confirmed this distribution. Thus, if any change with depth were to occur, a decrease due

to degradation on sinking or during collection in traps might be expected.

Chlorophyll *a*, expressed either as a concentration or as a percentage of total photosynthetic pigment content, is a sensitive measure of the deposition of phytogenous material. For example, enhanced chlorophyll *a* content in material settled in Bedford Basin during the winter and late spring reflects sedimentation of material derived from phytoplankton blooms at times when the biomass of herbivorous zooplankton (particularly microzooplankton) is small (Fig. 2, 4, and 5). These measures in sedimented material also decrease during the summer when the size of the zooplankton community that develops above 20 m is maximum. Deposition of fecal material produced by zooplankton grazing is of obvious importance for removal of phytoplankton from surface water during this time (Schrader 1971; Seki et al. 1974; Ferrante and Parker 1977). As discussed above, however, during the remainder of the year with low stratification and reduced populations of herbivores, sedimentation of particulate matter may involve other processes and pathways may not be direct. Then, as Murray (1970) suggests, turbulence, more than settling velocities of particles, may affect the vertical flux of particulate matter.

The importance of stratification and mixed-layer depth in determining the amount of annual carbon supply sedimented, demonstrated by comparing these variables in different water bodies, has been emphasized (Hargrave 1975). Our present study shows that within one location, seasonal changes in water column physical structure are related to both the amount and nature of particulate matter deposited at specific depths. Calculations of annual sedimentation do not adequately represent these seasonal differences which are of considerable importance for underlying benthic communities. If we consider the 20-m depth layer in Bedford Basin (Table 4), however, only a small fraction of particulate carbon added from various sources and assumed to be distributed evenly over the Basin surface is deposited. The proportion (15% of annual supply sedimented) is similar to other estimates for lakes (Kimmel and Goldman 1977; Wissmar et al. 1977) and coastal bays (Hargrave et al. 1976) where sedimentation was not measured near to the bottom and where terrigenous inputs are either not important or quantified separately.

These observations show that, considering the embayment as a whole, sedimentation accounts for a small fraction of total organic carbon flux through the surface waters of Bedford Basin. Also, sediments at all depths do not serve as a sink for deposited particulate matter to the same degree. Resuspension and redistribution of settled material can be significant processes that enhance mineralization of recently deposited sediments by delaying permanent burial (Wetzel et al. 1972; Hargrave and Kamp Nielsen 1977). In both large and small basins with sufficient water motion, these processes also transport deposited material to progressively deeper depths and cause accumulation in regions of reduced bottom slope gradient or at depths where turbulence is minimized. These postdepositional movements of sedimented material, which concentrate deposited material at specific depths and ultimately determine the distribution of organic and inorganic matter in bottom sediments, may be observable as anomalies in vertical profiles of sedimentation.

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Loss Rates of Suspended Material Sedimented in a Marine Bay[1]

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TAGUCHI, S., AND B. T. HARGRAVE. 1978. Loss rates of suspended material sedimented in a marine bay. J. Fish. Res. Board Can. 35: 1614–1620.

Loss rates for particulate carbon, nitrogen, chlorophyll *a*, and phaeophytin during the year in a coastal marine bay were calculated by comparison of sedimentation rates and suspended concentration of particulate matter available for deposition. Daily loss of carbon and nitrogen at various depths (1–6% with maximum values during late summer and autumn) generally decreased with depth and was highest when fecal pellet deposition increased during late summer. Loss rates of plant pigments were an order of magnitude lower than those of carbon and nitrogen, except when algal cells settled directly during winter. The observations substantiate previous assumptions that on a daily basis only a small proportion of suspended material is sedimented. Loss rate is dependent on the nature of the suspended particulate matter and physical structure of the water column.

Key words: sedimentation, suspended particulate matter, settling velocity, coastal embayment

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Nous avons calculé les taux de perte de carbone particulaire, d'azote, de chlorophylle *a* et de phéophytine au cours de l'année dans une baie de mer en comparant les taux de sédimentation et la concentration en suspension des matières particulaires disponibles pour déposition. La perte quotidienne de carbone et d'azote à diverses profondeurs (1 à 6% avec valeur maximum à la fin de l'été et en automne) diminue généralement avec la profondeur et ces valeurs sont à leur maximum quand la déposition des boulettes fécales augmente à la fin de l'été. Les taux de perte de pigments des plantes sont inférieurs d'un ordre de grandeur à ceux du carbone et de l'azote, sauf en hiver quand les cellules algales se déposent directement. Ces observations corroborent des hypothèses antérieures à l'effet que, sur base quotidienne, seulement une faible proportion des matières en suspension est déposée. Le taux de perte dépend de la nature des matières particulaires en suspension et de la structure physique de la colonne d'eau.

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MEASUREMENTS of sedimentation of particulate matter in different aquatic environments have been accompanied by simultaneous observations of the concentration of suspended material. When specific types of particles like diatom frustules or fecal pellets, or particulate element or energy content are compared, the average settling velocity may be calculated by dividing the sedimentation rate (taken as a measure of the settling flux) by the suspended concentration (Riley 1970; Burns and Pashley 1974; Ferrante and Parker 1977). Simultaneous observations of suspended concentration and deposition rates also allow calculation of the loss rate — the proportion of suspended concentration sedimented per unit time (Rigler 1973). This provides a relative basis for comparing removal rates by deposition since it normalizes sedimentation for differences in suspended concentrations. The comparison also indicates the degree to which deposition might be predicted from measures of suspended particulate concentrations.

Suspended and sedimented particulate matter have been monitored simultaneously (Stephens et al. 1967; Steele and Baird 1972; Ansell 1974). Except for calculations of particulate phosphorus loss (Rigler 1973) and fecal pellet sinking velocity (Ferrante and Parker 1977), the measures have not been combined to calculate loss rates and settling velocities. In this study we compare suspended and sedimented particulate matter measured at various depths in Bedford Basin during 1 yr to make these calculations. Changes in phytoplankton and zooplankton abundance, and stratification are

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identified as factors that determine seasonal and depth-related differences in the vertical flux of particulate matter in this coastal embayment.

Materials and Methods

Collection, analysis, and seasonal changes in suspended and deposited particulate matter in Bedford Basin are described in Hargrave and Taguchi (1978). Sedimentation, considered to be a measure of the vertical flux of particulate matter at any depth in the water column, was compared with the concentration of suspended matter averaged over time intervals during which sedimentation was measured. Biweekly sampling dates for suspended material did not always correspond with monthly sediment trap collection. Thus, the area under lines joining data points separated in time was calculated to estimate the time-averaged suspended concentration during trap exposures.

Measurements of sedimentation were compared with the measures of concentration of material suspended in water immediately above traps and with the total concentration integrated over the water column depths (20, 30, 40, and 60 m) at which traps were exposed. Such comparisons permit evaluation of the relative importance of suspended concentration (per cubic metre) in the vicinity of traps and the total concentration of suspended material available in the water column (per square metre) in determining deposition rates. Average daily sedimentation rates and corresponding time-averaged suspended particulate concentrations were then used to calculate an average daily loss rate (L) during a specific collection interval (i) by

$$(1) \qquad Li = \left[\frac{\frac{S_i}{n_i}}{\frac{\int_0^{n_i} C_i(t)dt}{n_i}} \right] 100$$

where S_i is total sedimentation per square metre during the i^{th} collection period of n days and C_i is the average time-integrated suspended particulate concentration (calculated per cubic metre or per square metre over n_i days). Daily sedimentation rates were thus expressed as a percentage of the average suspended particulate concentration potentially available for deposition from water at a particular depth and from the total water column.

Material settled in sedimentation traps is derived from a mixture of types of particulate matter with different material composition, decomposition rates, and settling velocities. However, specific settling velocities for separate components can be calculated since both suspended concentrations (C) and deposition rates (S) are known. Values of mean settling velocity (V) ($m \cdot d^{-1}$) are given by

$$(2) \qquad S = (V)(C)$$

Alternatively,

$$(3) \qquad V = \frac{(L_i)(Z)}{100}$$

where L_i is the daily loss rate expressed as a percentage and Z is water column depth (metres). These estimates do not assume that various components in particles settle separately, since a *total* settling velocity (by summation) is not calculated. However, the comparisons assume that diel variation in concentrations of suspended particulate matter (possibly through tidal exchange or vertical migration of organisms, as discussed by Naiman and Sibert 1977) are small relative to seasonal changes. Also, sedimentation at the end of a collection period is assumed to equal the sum of daily sedimentation. Differential utilization of various organic substrates during settling of particles and degradation or resuspension of settled material would alter sedimentation rates at different depths. Thus, deposition rates must be considered to be measures of the supply of nonlabile particulate matter intercepted by sediment traps in a manner analogous to that which occurs at the sediment surface.

Results and Discussion

Depth-Specific Loss Rates

Daily sedimentation rates (milligrams of various measures per square metre) at specific depths were usually of the same magnitude as average suspended particulate concentrations (milligrams per cubic metre) at the same depth. The average weight deposited also often exceeded suspended concentrations. Since concentrations of suspended particulate matter did not change greatly between consecutive sampling dates (Hargrave and Taguchi 1978), deposited material must have been derived from sources of supply in addition to suspended matter at depths where traps were suspended. Linear correlation analyses showed that only 3–15% of the seasonal variation in sedimentation of carbon, nitrogen, and plant pigments at all depths was attributable to variation in average suspended concentrations of these measures.

Depth-Integrated Loss Rates

While some deposited material is undoubtedly derived from suspended particles at depths of trap exposure, total suspended concentration in the water column above a given depth provides a more appropriate measure for calculation of loss rate. Even if sedimentation is due to variable supply of particulate matter from horizontal advection and vertical settling (Hargrave and Taguchi 1978), concentrations of suspended material integrated over depth may be representative of the total supply available for deposition.

Seasonal values of daily loss rate for particulate carbon and nitrogen, integrated above depths at which sedimentation was measured, varied from $<1\%$ to a maximum of 6% (Fig. 1). Values were generally similar except during late summer and early fall when nitrogen loss rates were slightly increased. Similar values occurred at all depths except during periods of stratification (June–September) when highest daily loss through sedimentation occurred for material suspended above 20 m. A second period of maximum loss occurred at 40 m during September.

Daily loss of suspended chlorophyll *a* and phaeophytin integrated over various depths was usually an order of magnitude less than rates observed for par-

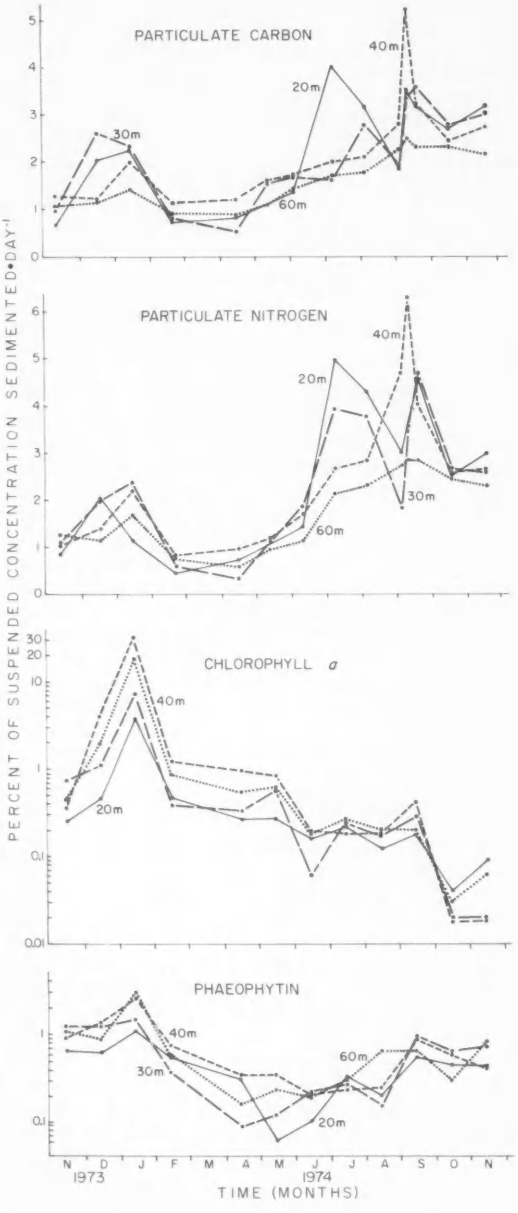

FIG. 1. Daily percentage loss rates of suspended particulate carbon, nitrogen, chlorophyll *a*, and phaeophytin through sedimentation at various depths in Bedford Basin. Average daily sedimentation rates are expressed as a percentage of average suspended concentrations available for deposition from the total water column above the depth and during the period of sediment trap exposure. Sedimentation rates and measures of suspended concentrations are given in Hargrave and Taguchi (1978, fig. 1).

TABLE 1. Index of determination (r^2) derived from linear regression analyses comparing loss rate of particulate matter deposited throughout the year at different depths in Bedford Basin (data in Fig. 1).

	Depth (m)	30	40	60
Carbon	20	.59	.42	.57
	30		.52	.66
	40			.72
Nitrogen	20	.84	.34	.66
	30		.44	.67
	40			.70
Chlorophyll *a*	20	.97	.98	.98
	30		.95	.95
	40			.99
Phaeophytin	20	.76	.81	.71
	30		.70	.76
	40			.60

ticulate carbon and nitrogen (Fig. 1). Except for maximum values during January, when daily sedimentation of chlorophyll *a* and phaeophytin at various depths was equivalent to between 3 and 30% of suspended concentrations, daily loss did not exceed 1%. Loss during late spring and summer was approximately constant at $0.2\% \cdot d^{-1}$. Loss rates for plant pigments were also similar at all depths except during winter and late spring when higher values tended to occur at deeper depths.

No clear relation existed between seasonal changes in daily loss rate and concentrations of suspended material. Annual maximum loss rates for plant pigments during January, for example, followed a period of increased pigment concentration (fig. 1, Hargrave and Taguchi 1978). On the other hand, high concentrations of chlorophyll *a* during late March and phaeophytin during late summer were not reflected in subsequent increases in loss rate. Also, no increases in suspended carbon or nitrogen occurred during late summer and early autumn when loss rates of these substances were maximum.

There was no clear trend to values of loss rate with increasing depth which was common to all four substances (Fig. 1). Values for particulate carbon and nitrogen generally decreased with increasing depth but there was no depth-dependent pattern for loss of plant pigments. Loss rates of chlorophyll *a* were high and increased with depth (to highest values at 40 and 60 m) only during January. A similar depth-specific increase in particulate carbon and nitrogen loss rate occurred at 40 m during September. Horizontal advection could have enhanced deposition at these depths.

Despite the conclusion that sedimentation of particulate matter in Bedford Basin is not only due to vertically settling particles, loss rates for various substances may be compared by correlation analyses to indicate similarities in seasonal changes between depths (Table 1). Highest coefficients of r^2 occurred for chlorophyll *a*,

TABLE 2. Coefficients of variation (as percent) of suspended concentrations and sedimentation of organic carbon, nitrogen, chlorophyll *a*, and phaeophytin measured over various depth intervals in Bedford Basin during 1973–74. Measures of suspended concentrations (n = 38) and sedimentation (n = 12) are given in Fig. 1 (Hargrave and Taguchi 1978).

	Suspended concn				
Depth interval (m)	0–20	20–30	30–40	40–60	$\bar{x}$ C.V. as %
Carbon	36.5	32.6	29.7	26.0	31.2
Nitrogen	40.9	37.4	34.3	30.7	35.8
Chlorophyll *a*	70.3	76.0	76.1	75.4	74.7
Phaeophytin	55.7	48.9	48.0	51.4	50.9
	Sedimentation rate				
Depth interval (m)	20	30	40	60	$\bar{x}$ C.V. as %
Carbon	48.4	48.2	46.1	39.5	45.6
Nitrogen	59.3	56.5	57.5	45.4	54.7
Chlorophyll *a*	122.8	156.1	179.9	211.1	167.5
Phaeophytin	74.0	102.5	134.7	88.6	97.3

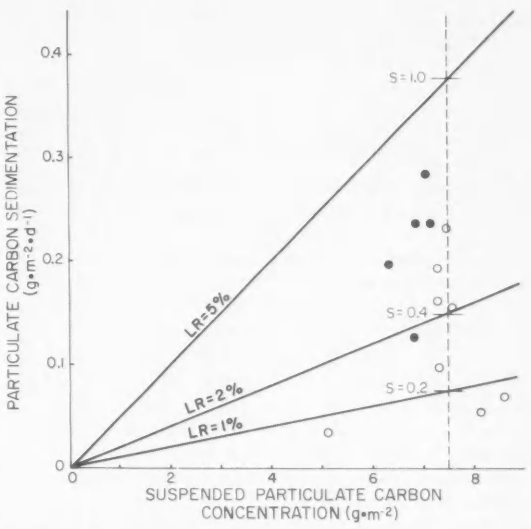

FIG. 2. Comparison of average suspended concentrations and sedimentation rates of particulate carbon at 20 m during various collection periods throughout the year in Bedford Basin. Heavy lines indicate the relation between suspended concentration and sedimentation rate for different daily loss rates (LR). Equivalent settling velocities (S) as (metres per day) for a particulate carbon concentration of 7.5 g·m^{-2}. Solid points represent data collected at 20 m during periods of stratification.

where seasonal changes in loss rate at one depth are directly related to those at all other depths. Loss of phaeophytin at different depths showed similar, though slightly lower, coherence between all depths. Loss rates of particulate carbon and nitrogen, on the other hand, while also showing similar seasonal trends (Fig. 1), with some exceptions, were not correlated to the same degree. For example, loss rates for nitrogen between 20 and 30 m are well correlated seasonally, while this is less so for particulate carbon (Table 1).

Quantitative Comparisons of Suspended Concentrations and Deposition Rates

Since values of loss rate are calculated from a ratio (sedimentation/suspended concentration), an equivalent change in both numerator and denominator will not alter the ratio. Alternatively, differences in the ratio may be largely attributable to changes in only one of the variables if the other is relatively constant. Comparisons of annual variation in suspended concentrations and sedimentation rates at different depths indicate that variation in suspended concentrations of particular substances was always less than variation in sedimentation rates (Table 2). The difference was small for carbon and nitrogen and total annual variation of both suspended concentration and deposition rate decreased slightly with increasing depth. Variation in suspended pigment concentrations, on the other hand, was approximately double that for carbon and nitrogen and seasonal variation in sedimentation was also 2–3 times higher. Greater variation tended to occur with increasing depth.

The small seasonal variation in suspended particulate concentrations relative to that in sedimentation rates can be further demonstrated by a plot of values of the two variables for one depth (20 m) during various collection periods (Fig. 2). The cluster of points illustrates the small changes in suspended particulate carbon concentration which are not directly correlated with much larger seasonal changes in deposition. Highest loss rates of particulate carbon at 20 m occurred during periods of stratification (July–September). Suspended concentrations of particulate carbon were below the annual depth integrated mean (7.0 g C·m^{-2}) during this time, but net zooplankton biomass and microzooplankton volume was high (fig. 5, Hargrave and Taguchi 1978). On the other hand, highest concentrations of suspended particulate carbon (above 8 g·m^{-2} during March–April and October–November) were not associated with increased sedimentation rates. Similar comparisons for particulate nitrogen and plant pigments also illustrated that sedimentation rates were not positively correlated with seasonal changes in concentrations of suspended matter.

Settling velocity calculated on the basis of measured components of particulate matter is derived from the product of loss rate and depth over which sinking can occur (equation 3), thus seasonal trends in values of settling velocity were similar to those for loss rate. High settling rates of chlorophyll *a* (0.05–5 m·d^{-1}) which increased with depth only during January paralleled similar trends for loss rate. Throughout the remainder of the year, and particularly during the late summer

and fall, values for particulate carbon loss (1–5% $\cdot d^{-1}$) were equivalent to settling velocities of 0.1–1 m $\cdot d^{-1}$ (Fig. 2).

Relations Between Loss Rate and the Nature of Deposited Material

Hargrave and Taguchi (1978) discussed seasonal differences in the origin of deposited material in Bedford Basin. Zooplankton fecal production during mid- to late-summer is observable in enhanced values for loss rate of particulate carbon and nitrogen (Fig. 1). Similarly, direct sedimentation of algal cells during winter leads to increased loss rates of plant pigments (especially chlorophyll *a*). However, counts of fecal pellets and diatom frustules deposited per day at different depths between June and November (Hargrave et al. 1976; fig. 2 in Hargrave and Taguchi 1978) were not significantly correlated with estimates of loss rate. These observations imply that while deposition of fecal pellets and algal cells in Bedford Basin may be seasonally important, observed loss rates of particulate matter largely reflect the deposition of other material. Alternatively, seasonal changes in the composition of suspended particulate matter (through phytoplankton production and zooplankton feeding, for example) could impart differences in settling velocity which are reflected in variable loss rates. In any case, maximum values of loss rate for particulate carbon and nitrogen during late summer and chlorophyll *a* during winter are conservative estimates of these measures for fecal pellets and algal cells. Amorphous debris and inorganic particles were present in different amounts throughout the year (Hargrave and Taguchi 1978). Values for loss rate must reflect this variable composition.

Sedimented chlorophyll *a* may be converted to organic carbon, assuming a factor of 30 (Strickland 1960), to further demonstrate the extent to which phytoplankton contribute to deposited material. During periods of maximum chlorophyll sedimentation (winter and spring), from 1 to 3 mg chlorophyll $a \cdot m^{-2} \cdot d^{-1}$ (30–90 mg $C \cdot m^{-2} \cdot d^{-1}$) was deposited. Total particulate carbon deposition during these periods was approximately 200 mg $\cdot m^{-2} \cdot d^{-1}$ (fig. 1, Hargrave and Taguchi 1978). Thus, phytoplankton could have accounted for from 15 to 45% of the carbon deposited. Over the remainder of the year, however, chlorophyll deposition was below 0.2 mg $\cdot m^{-2} \cdot d^{-1}$ (1.5 mg $C \cdot m^{-2} \cdot d^{-1}$) while total particulate carbon sedimentation usually exceeded 200 mg $C \cdot m^{-2} \cdot d^{-1}$. Phytoplankton obviously contributed little to the direct deposition of particulate matter during these periods, as values for chlorophyll *a* loss rate indicate.

General Discussion

Previous studies that have attempted to describe the dynamics of natural phytoplankton populations and suspended particulate material have either assumed or calculated a small constant daily loss through sedimentation (Lund et al. 1963; Vollenweider 1966; Platt and Conover 1971; Jassby and Goldman 1974). Nakajima and Nishizawa (1972) estimated that a daily elimination of 2–4% of suspended particulate carbon would be required to achieve the exponential decrease observed in the surface waters of the Bering Sea. Interestingly, similar rates for calorific loss of seston were calculated by Hutchinson (1938) to account for oxygen loss in the stratified hypolimnia of two lakes. Rigler (1973) commented on the similarity of these loss rates and phosphorus loss from the trophogenic zone of different lakes where between 1 and 3% of suspended phosphorus sedimented daily. The distribution of mercury in Lake Ontario sediments can also be accounted for if the rate of mercury transfer to sediments is assumed to be proportional to its concentration in the water column (Boyce 1974).

Daily loss rates of particulate carbon and nitrogen observed in Bedford Basin are similar to these values, but to some extent the correspondence may be fortuitous. Toyoda et al. (1968), Steele and Baird (1972), and Ansell (1974) noted no consistent correlation between sedimentation and concentrations of suspended carbon but loss rates were not calculated. Estimates of daily loss from $<1\%$ to over 50% may be calculated from their data and from that presented by Stephens et al. (1967). High values, however, are associated with sedimentation measured near the bottom or at times of year when runoff added terrestrially derived material. High rates of sedimentation under such conditions can usually be attributed to the rapid sinking of inorganic particles (Patten et al. 1966; Trevallion 1967; Koidsumi and Sakurai 1968; Oviatt and Nixon 1975). Daily loss rates calculated from these studies for depths closer to the surface and during stratification, when resuspension may be less important, were usually $<10\%$.

Even though this and previous studies indicate no fixed proportionality between suspended concentration and sedimentation rates, it is apparent from Fig. 2 that values for loss rates may vary within narrow limits when changes in suspended concentration are small relative to those in deposition rate. It is also clear that loss rates depend on the nature of suspended particles and water column physical structure. Thus, highest loss rates (5% $\cdot d^{-1}$) for particulate carbon and nitrogen occurred during summer stratification, a time when fecal pellets were abundant in deposited material (Hargrave and Taguchi 1978). High settling velocities of zooplankton fecal pellets (Smayda 1970; Ferrante and Parker 1977) suggest why this occurs. On the other hand, loss rates of plant pigments, especially chlorophyll *a*, in Bedford Basin, were reduced during stratification.

These estimates of the vertical flux of suspended particulate matter should be compared realizing that sinking rates in still water are different from apparent sedimentation caused by net downward velocity through advection. Numerous previous studies have reported

that turbulence and mixing reduce loss and may even permit dense particles such as diatoms to remain in suspension (Lund 1959; Smayda 1970). Lund et al. (1963) described changes in the phytoplankton concentration in Lake Windermere that demonstrate this effect. Distribution profiles of living and dead *Asterionella* indicated that epilimnetic turbulence kept cells in suspension but those cells entering the pycnocline were removed by passive sinking. Riley (1970) also stressed that suspended material may have an apparent sinking rate due to a net downward vertical velocity.

Our estimates of daily loss rate are similar to other measures determined in situ. Burns and Pashley (1974) suspended double-chambered cylinders at various depths in Lake Ontario to measure sinking rates of suspended particulate carbon and phosphorus. Particulate matter usually settled in cylinders but samples from above the thermocline often displayed upward movement presumably due to mobility of organisms. Sinking rates were between 0.1 and 2.5 $m \cdot d^{-1}$ below the thermocline, values similar to those derived from estimates of loss rate in our study and calculated by Riley (1970) for aggregates and small particles settling in seawater. Flux of phosphorus across the thermocline in Burns and Pashley's study removed 0.1–5% of suspended particulate phosphorus from the upper mixed layer after stratification.

High daily loss rates for chlorophyll *a*, particularly in deep water during December and January, imply a nonvertical supply of deposited material in Bedford Basin (Fig. 1). Concentrations of suspended chlorophyll were reduced throughout the water column following a peak during early December (Hargrave and Taguchi 1978). Intermittent processes that transported chlorophyll *a*, accumulated either on the sediment surface or in density gradients within the water column, could enhance deposition at particular depths. If changes in suspended concentration were not detected in the biweekly samples, high loss rates and settling velocities would be calculated for the low suspended concentrations measured. This phenomenon could also account for high correlations observed in chlorophyll *a* loss rate between depths throughout the year (Table 2).

While there was no clear trend of loss rate of suspended plant pigments with depth in our study, lower loss rates of particulate carbon and nitrogen usually occurred at the deeper depths (Fig. 1) where vertical mixing is likely to be minimum. Resuspension of bottom sediments from the sides of the basin, apparent in increased deposition at deeper depths (Hargrave and Taguchi 1978), may add material to the water column. If this was of high density, as seems likely, increased loss rate with increasing depth might be expected. Anomalies of increased loss rate at intermediate depths occurred, however (Fig. 1). Since the measure of loss rate represents sedimentation normalized for suspended concentration, these instances of high loss rate are not attributable to changes in concentration of suspended material. This supports the idea that at certain times material trapped at various depths in Bedford Basin may be of different origin which reflects horizontal and vertical processes of supply. It is thus inappropriate to interpret vertical differences in loss rate further. The observations also substantiate previous assumptions (Platt and Conover 1971) that on a daily basis sinking removes a small proportion of suspended particulate matter in Bedford Basin.

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Seasonal Changes in Oxygen Uptake by Settled Particulate Matter and Sediments in a Marine Bay[1]

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Oxygen consumption by material deposited in sediment traps suspended at different depths in a coastal marine bay was highest during summer. Seasonal changes in respiration (Formalin sensitive oxygen uptake) were significantly correlated with organic content and highest rates on a dry and organic weight basis occurred during summer. There was no consistent depth-related change in oxygen uptake but seasonal changes in respiration were significantly correlated over consecutive 10-m depth intervals between 20 and 60 m. Rates of respiration and chemical oxidation by undisturbed sediment cores from 60 m, which were maximum during late summer, were not related to seasonal changes in temperature or dissolved oxygen concentration. A 1–2-mo delay existed between the deposition of particulate matter with maximum rates of oxygen consumption and maximum oxygen uptake by bottom sediments. Similar seasonal changes and calculation of the carbon equivalent of sediment respiration, however, show that oxidation of settled organic matter is largely complete within the year of deposition.

Key words: sedimentation, particulate matter, biological and chemical oxidation, marine sediments

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La consommation d'oxygène par les matières déposées dans des trappes à sédiments suspendues à différentes profondeurs dans une baie de mer atteint un sommet en été. Les changements saisonniers dans la respiration (absorption d'oxygène sensible à la formaline) ont une corrélation significative avec la teneur en matière organique, et les taux maximums sur la base du poids sec et organique se produisent en été. Il n'y a pas de changement uniforme en fonction de la profondeur dans l'absorption de l'oxygène, mais on a pu établir des corrélations entre les changements saisonniers dans la respiration à des intervalles consécutifs de 10 m, entre 20 et 60 m. Les taux de respiration et d'oxydation chimique dans des carottes de sédiment non dérangé prélevées à 60 m, qui étaient à leur maximum vers la fin de l'été, ne montrent pas de relation avec les changements saisonniers dans la température ou la teneur en oxygène dissous. Il y a un décalage de 1 à 2 mo entre la sédimentation des matières particulaires avec taux maximums de consommation d'oxygène et l'absorption maximum d'oxygène par les sédiments benthiques. Des changements saisonniers semblables et le calcul de l'équivalent carbone de la respiration des sédiments indiquent toutefois que l'oxydation de la matière organique déposée est en grande partie terminée avant la fin de l'année de sédimentation.

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DEPLETION of dissolved oxygen occurs in any body of water when oxygen uptake by suspended and settled material exceeds the rate of oxygen supply (Birge 1908). Thus, oxygen deficits formed within a water mass have been used to estimate the supply of oxidizable material that would be necessary to produce an observed rate of oxygen depletion (Hutchinson 1957; Lund et al. 1963; Riley 1970). Oxygen uptake by settled material and sediments, however, can also be measured directly. Studies by Thomas (1955) combined both types of measurement to show that, on a volume basis, the oxygen deficit formed in the stratified hypolimnia of three lakes approximated oxygen consumed by material collected in sediment traps when this was stirred in bottles filled with oxygenated water. This is the only work to date that has combined a functional measurement (oxygen uptake) of settled material with measures of concentration of particulate matter deposited per unit time.

[1]Bedford Institute of Oceanography Contribution.

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Collections of material settled in cylinders moored at various depths in Bedford Basin (Hargrave and Taguchi 1978) provided samples of particulate matter that were used for measurements of oxygen uptake reported here. The measure quantifies the susceptibility of organic matter to oxidation and it may characterize the degree to which particulate debris has decomposed (Hargrave and Phillips 1977). Oxygen depletion regularly occurs in water below sill depth (20 m) during periods of stratification in Bedford Basin (Hargrave et al. 1976), but an areal oxygen deficit cannot be calculated because of intermittent mixing. However, oxygen consumption by undisturbed sediment cores collected from below moored sediment traps was measured. Seasonal changes in these rates were compared with oxygen uptake by freshly deposited particulate matter to examine the relationship between oxygen consumption by bottom sediments and the supply of particulate organic matter susceptible to oxidation.

Materials and Methods

Collection and analyses of material settled in sediment traps moored on a fixed wire at various depths in Bedford Basin are described in Hargrave et al. (1976). No preservatives were added to prevent decomposition. Metabolic poisons could not be used since total (both biological and chemical) oxygen uptake by the settled material was to be determined. Within 1 h of collection, supernatant water in cylinders was decanted and settled particulate matter in one cylinder from each depth was used for measures of total and chemical oxygen uptake.

Water used for incubations was collected at 20 m in Bedford Basin and equilibrated by stirring for 24 h at 10°C after filtration and addition of Formalin to a subsample to yield a 1% solution. Preliminary experiments showed that with 50–100 mg dry weight of particulate matter suspended in 30 mL, changes in dissolved oxygen concentration were linear over 18 h when 10–30% of the oxygen was consumed. Incubations, in the dark at 10°C with glass-stoppered bottles continuously rotated at 30 rpm, seldom exceeded this time and differences in dissolved oxygen in water in blank (without sediment) and sample flasks measured with a Radiometer Blood Gas Analyzer were used to calculate absolute changes in concentration per hour. Determination of dry weight of sediment in each flask, and measures of organic carbon and nitrogen in subsamples permitted calculation of total and chemical oxygen uptake on the basis of either dry or organic weight (Hargrave et al. 1976). Respiration is assumed to be measured by the difference between oxygen uptake with and without Formalin treatment.

Undisturbed cores of sediment (20–25 cm long) with overlying water (10 cm) were collected at 3–4-wk intervals during the time that sediment traps were in place. Cores of soft silt, clay sediment were taken at 60 m depth near the site at which sedimentation was measured in the central part of Bedford Basin. A Kajak corer was used to collect four cores on each occasion and they were incubated in a dark refrigerator at in situ temperatures. Teflon-coated magnetic stirrers, mounted in stoppers used to cap cores, were rotated by induction from a large magnet. This ensured homogeneous concentrations of dissolved oxygen in water over the sediment. Syringes were used to take 2-mL samples through a septum in the stopper for analysis before and after a 6–10-h incubation. The needle of a second syringe (25 mL), filled with filtered seawater, also passed through the septum. This reservoir served to compensate for water withdrawn on sampling. It also permitted injection of a volume of concentrated buffered Formalin in seawater sufficient to give a 1% concentration. Injections were made after measurements of total oxygen uptake, with a 1-h equilibration before residual oxygen consumption was measured. Rates of oxygen uptake were expressed as mg $O_2 \cdot m^{-2} \cdot h^{-1}$ before and after Formalin addition.

Results and Discussion

Seasonal Differences in Oxygen Uptake by Settled Particulate Matter

Average values of oxygen consumption by sedimented particulate matter during fall and winter (0.1–0.5 mg $O_2 \cdot g^{-1} \cdot h^{-1}$) increased three- to fourfold during May (Fig. 1). Variation (±SD) in rates of uptake by material deposited at different depths was also greatest between

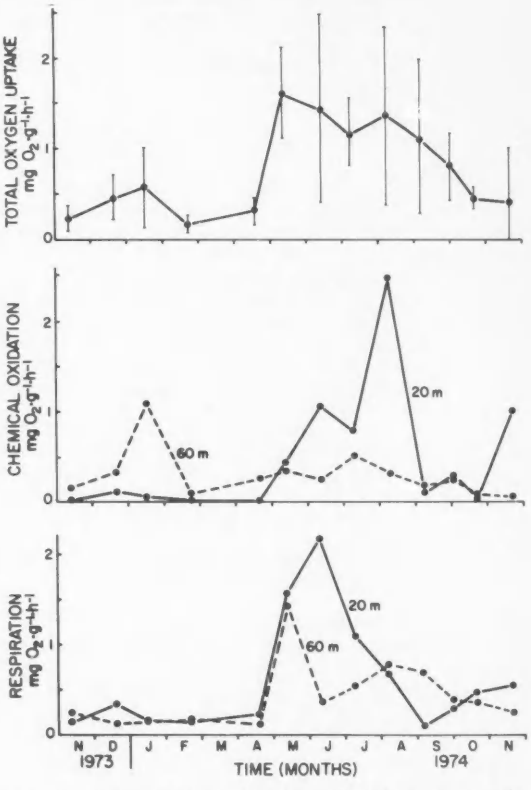

FIG. 1. Average values (±1 SD) of total oxygen uptake by material deposited at different depths ($n = 5$) throughout the year in Bedford Basin. Chemical oxidation (residual after poisoning with Formalin) was subtracted from total oxygen uptake to estimate biological respiration.

June and September when the water column was stratified. Maximum rates of oxygen uptake occurred in material collected at 20 m between June and August. This would be expected if the concentration of oxidizable material in particulate matter deposited at 20 m was higher than at other depths. At other times, however, there was no consistent trend with depth and often oxygen uptake was highest at intermediate depths. Hargrave and Taguchi (1978) have discussed nonvertical transport and in situ production of particulate matter which may enhance deposition at particular depths in Bedford Basin.

Oxygen uptake, measured as chemical and biological consumption, also showed seasonal and depth-related differences (Fig. 1). Except for high rates of chemical oxidation at 60 m during January, these measures were similar throughout the winter. After May, however, when respiration increased and accounted for over 70% of the total oxygen uptake in material settled at all depths, differences between depths appeared. Highest rates of biological and chemical oxidation occurred at 20 m during June and August, respectively. A small secondary peak in respiration in material settled at 60 m during late summer was not observed for particulate matter deposited at 20 m. Also, chemical oxygen uptake increased at 20 m during the summer while remaining approximately constant in material settled at 60 m. The seasonal differences clearly show variations in the nature of the processes involved and susceptibility of settled material to oxidation at different depths.

Depth-Related Differences in Oxygen Uptake by Settled Particulate Matter

Correlation analyses were used to compare oxidation of material settled seasonally at various depths (Table 1). There was low coherence in rates of total and chemical oxygen uptake by material deposited at different depths except for measurements at 40 and 50 m. In contrast, measures of respiration in particulate matter settled at 10-m depth intervals were significantly correlated ($r^2 > 0.50$). In some cases (30–50 m, 40–60 m) the seasonal changes were correlated over a 20-m depth interval. There was, however, no depth-dependent trend to these correlations. Some trend with depth might be expected if a seasonal supply of readily oxidized material occurred with particulate matter originating above 20 m.

Table 1. Index of determination (r^2) from linear regression analyses comparing oxygen uptake by particulate material collected in sediment traps at different depths throughout the year in Bedford Basin. $n = 13$ in all regressions.

Depth (m)	30	40	50	60
		Total oxygen uptake		
20	0.26	0.08	0.06	0.02
30		0.27	0.35	0.10
40			0.88	0.22
50				0.38
		Chemical oxidation		
20	0.49	0.04	0.09	0.008
30		0.006	0.12	0.01
40			0.88	0.006
50				0.05
		Respiration		
20	0.63	0.18	0.22	0.02
30		0.74	0.77	0.13
40			0.84	0.67
50				0.54

Comparison of Organic Content and Oxygen Uptake

Previous studies have established relationships between rates of oxygen uptake, surface, area and organic content of sediments and particulate matter from marine and freshwater areas (Hargrave 1972; Hargrave and Phillips 1977). Chemical oxidation in sediments is assumed to reflect oxygen uptake by reduced organic and inorganic substances (Pamatmat 1971). Thus, increased chemical oxidation of material settled in traps at 20 m but not at 60 m during the summer (Fig. 1) could indicate accumulation of reduced compounds through anaerobic activity in material deposited at the shallower depth. No significant correlation existed between sediment organic content (weight loss on ashing at 500°C) and chemical oxidation by material settled at various depths, however. Presumably reduced compounds present in both organic and inorganic matter contribute to oxygen uptake residual after poisoning.

Respiration, on the other hand, was generally significantly correlated with total organic, carbon, and nitrogen content when data collected throughout the year were grouped or analyzed on a depth-specific basis (Table 2). Correlation coefficients were highest for material collected at 60 m and grouping of data from all depths decreased the amount of variance attributable to organic content. A stepwise multiple regression that compared all three measures of organic matter (which themselves were highly correlated, $r^2 > 0.90$) and respiration showed that variance was not decreased significantly by inclusion of variables other than organic carbon in the regression. There was also no significant trend in values of slope coefficients with depth. Arithmetic mean slope values (±1 SD) for regressions of respiration on organic matter (0.044 ± 0.010), carbon (0.076 ± 0.020), and nitrogen (0.342 ± 0.076) in particulate matter were similar to those derived by grouping data collected from all depths (Table 2).

Respiration in settled material was calculated on an organic weight basis to indicate seasonal differences in rates of oxidative decomposition due to other factors. A peak and subsequent decrease in respiration per gram nitrogen in material settled during May (Fig. 2) corresponds to a similar seasonal trend in the amount and proportion of total pigment as chlorophyll *a* presents in

TABLE 2. Intercept (a) and slope (b) coefficients and index of determination (r^2) of linear regressions for comparison of percent organic matter (weight loss on ignition), organic carbon, and nitrogen and oxygen uptake (respiration) by material settled in sediment traps at different depths in Bedford Basin. n = number of observations collected throughout the year. All correlations are significant ($P < 0.05$) except those marked with an asterisk.

Depth (m)	n	a	b	r^2
		Organic matter		
20	13	−0.50	0.041	0.33
30	14	−0.28	0.029	0.26*
40	14	−0.64	0.050	0.60
50	12	−0.76	0.052	0.61
60	12	−0.83	0.050	0.90
All depths	65	−0.55	0.042	0.43
		Organic carbon		
20	13	−0.17	0.080	0.50
30	14	0.02	0.045	0.24*
40	14	−0.25	0.092	0.56
50	12	−0.28	0.092	0.52
60	12	−0.20	0.070	0.79
All depths	65	−0.15	0.073	0.45
		Nitrogen		
20	13	0.04	0.391	0.41
30	14	0.17	0.211	0.19*
40	14	0.13	0.339	0.38
50	12	0.08	0.376	0.27*
60	12	−0.05	0.392	0.79
All depths	65	0.08	0.334	0.34

deposited particulate matter (Hargrave and Taguchi 1978). Enhanced respiration between December and February also coincides with a secondary peak in chlorophyll *a* in settled material during winter. This implies that living phytoplankton contributed significantly to respiration of settled material during these periods. Increased respiration in material deposited at 60 m during May, with no increase in chemical oxidation (Fig. 1), also provides evidence for the presence of living organisms. Carbon/chlorophyll *a* ratios in this material were between 150 and 400, the lowest observed through the year. However, there was no significant correlation between respiration per gram nitrogen and organic carbon as percent of organic matter or carbon/nitrogen ratios in the material deposited.

Rates of respiration expressed per unit organic matter, organic carbon, or nitrogen should be correlated because the measures of organic content are significantly correlated themselves. Hargrave and Phillips (1977), however, showed that communities of organisms that colonized glass surfaces developed stable biomass and metabolic levels over time. A linear relation between respiration calculated on the basis of weight of carbon and nitrogen present in communities was observed during a 14-mo period of colonization when respiration decreased asymptotically from 200 mg $O_2 \cdot g^{-1}$ $N \cdot h^{-1}$ (30 mg $O_2 \cdot g^{-1}$ $C \cdot h^{-1}$) to 40 mg

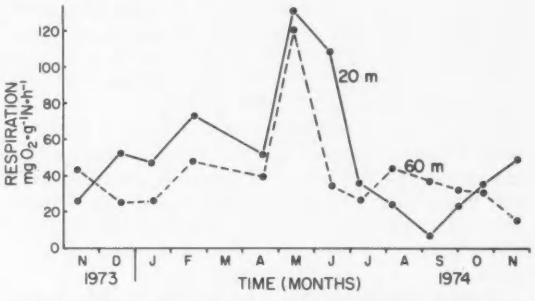

FIG. 2. Biological respiration of particulate matter settled at two depths throughout the year in Bedford Basin (from Fig. 1) expressed per gram nitrogen in deposited material.

$O_2 \cdot g^{-1}$ $N \cdot h^{-1}$ (5 mg $O_2 \cdot g^{-1}$ $C \cdot h^{-1}$). Similar time-dependent changes and stable rates of oxygen uptake were observed in decomposing detritus and invertebrate feces (Hargrave 1976). Identical rates exist for biological respiration of settled particulate material collected from Bedford Basin averaged annually over all depths (44 mg $O_2 \cdot g^{-1}$ $N \cdot h^{-1}$ and 5.5 mg $O_2 \cdot g^{-1}$ $C \cdot h^{-1}$). Stable levels of respiration could result from biostasis in microbial communities due to reduced availability of space and nutrients. If this is so, sediments at 60 m in Bedford Basin only receive a supply of particulate matter that consumes oxygen above basal rates during May (Fig. 2).

OXYGEN UPTAKE BY UNDISTURBED SEDIMENTS

In contrast to oxygen consumption by settled particulate matter, total oxygen uptake by undisturbed sediment cores increased gradually during spring, and maximum rates occurred during July and August (Fig. 3). Maximum rates of chemical oxidation in cores, about 40% of total uptake, occurred early in August. There was no consistent trend in the proportion of total oxygen consumption due to chemical uptake. Both measures decreased rapidly during late summer to minimum values in November.

These seasonal changes were not clearly related to variations in concentration of dissolved oxygen in water above the sediment, although a rapid decrease in oxygen uptake after August coincided with a reduction in dissolved oxygen concentration (Fig. 3). However, approximately constant rates of oxygen consumption were maintained throughout winter months when dissolved oxygen concentration also decreased. Annual changes in oxygen uptake were also unrelated to small changes in temperature. Maximum temperature (4°C) occurred at 60 m during winter and fall when the water column was well mixed. These were times of minimum oxygen uptake by sediment cores.

Since sediment oxygen uptake varied independently of these physical variables, seasonal changes in oxygen consumption by sediment cores might be compared

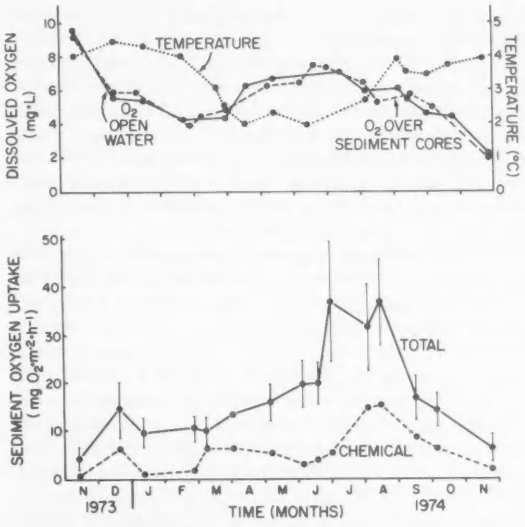

FIG. 3. Seasonal changes in temperature and dissolved oxygen concentration in water and total and chemical oxygen uptake by undisturbed sediment cores collected from 60 m in Bedford Basin. Vertical lines ±SD of the mean.

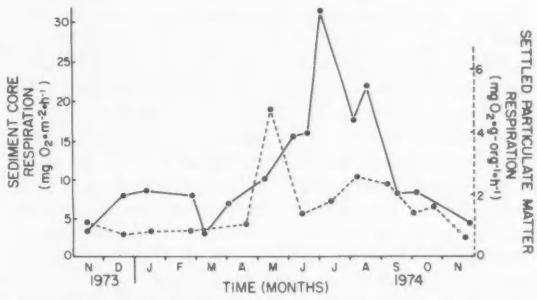
SEDIMENT CORE RESPIRATION (mg O2·m-2·h-1)
SETTLED PARTICULATE MATTER RESPIRATION (mg O2·g-org·h-1)
N D J F M A M J J A S O N
1973
1974
TIME (MONTHS)

FIG. 4. Biological respiration (calculated as the difference between total and chemical oxygen uptake, Fig. 3) by undisturbed sediment cores and biological respiration per gram organic matter in particulate matter settled at 60 m in Bedford Basin throughout the year.

with rates of oxygen consumption of settled particulate matter to test the idea that the supply of oxidizable material affects seasonal changes in benthic oxygen consumption. Highest rates of chemical oxygen uptake by material settled at 60 m during January (Fig. 1) did not coincide with maximum chemical oxidation by bottom sediments during August (Fig. 3). Maximum respiration per gram organic matter in material settled during May also preceded the summer peak in sediment core respiration by 6 wk (Fig. 4). Both measures declined after August to minimum values in November. Thus, if respiration in bottom sediments was enhanced by deposition of organic matter susceptible to oxidation, stimulation was not immediate and the effect did not extend beyond the end of the summer.

TABLE 3. Comparison of organic carbon sedimentation and the carbon equivalent of sediment core respiration at 60 m in Bedford Basin during 1974.

Date	Sedimentation[a] g C·m^{-2}	Sediment core respiration[b] g O_2·m^{-2}	Sediment core respiration[b] g C·m^{-2}
Jan. 1–April 30	16.3	46.8	14.9
May 1–Sept. 30	37.6	118.5	37.8
Oct. 1–Dec. 31	21.8	132.5	10.3
Total (annual)	75.7	197.8	63.0

[a]Hargrave and Taguchi (1978).
[b]Hourly rates (Fig. 4) converted to monthly totals assuming no diel differences in respiration and R.Q. = 0.85. Conversion to carbon equivalents assuming respiratory quotient (RQ) = 0.7–1.0 would alter values ±17%.

The degree to which deposited organic matter is oxidized may be estimated by comparison of organic carbon sedimentation with the carbon equivalent of sediment respiration (Table 3). The conversion of oxygen uptake necessitates assumption of a respiratory quotient. A value of 0.85 was chosen since respiratory oxygen consumption was measured. The conversion shows that organic carbon requirements for sediment respiration are balanced by measured rates of supply between January and September when 90–100% of the organic matter deposited was respired. Only 47% of material settled between October and December was respired aerobically. On an annual basis, sediment respiration was equivalent to 83% of organic carbon supply. Respiratory quotient (RQ) values are probably not constant through the year since organic matter may be metabolized anerobically (Davies 1975; Pamatmat 1977). The calculations do indicate, however, that utilization approximates organic carbon input to these sediments.

General Discussion

Thomas (1955) measured oxygen uptake by particles deposited in collectors suspended at single depths throughout the year in three Swiss lakes. Rates of total oxygen uptake (calculated from his data) varied from 0.2 to 2.8 mg $O_2 \cdot g^{-1} \cdot h^{-1}$ with maximum rates during July in eutrophic lake Pfäffikersee. Oxygen consumption by material settled in oligotrophic Aegerisee was more constant throughout the summer (1 mg $O_2 \cdot g^{-1} \cdot h^{-1}$) with rates during winter reduced by 90%. Similar seasonal patterns and rates of oxygen uptake were observed for material settled in Bedford Basin (Fig. 1) where increased oxygen consumption also occurred during summer, but high rates of respiration and chemical oxidation did not coincide. Both studies show temporal variation in the supply of oxidizable particulate matter with greatest differences during summer stratification.

Other studies have also indicated the importance of seasonal stratification in determining the balance between production and respiratory consumption of particulate organic matter in a water column (Hutchinson 1957). Measurements or calculations that estimate mineralization of photosynthetically fixed carbon show that up to 90% may be regenerated in the upper 200 m of the sea (Riley 1970). Similarly, the bulk of decomposition of particulate organic matter suspended in lakes occurs in the epilimnion during summer (Kleerekoper 1953; Ławacz 1969; Bloesch et al. 1977). Rapid degradation of organic matter in surface waters is also evident from measurements of sedimentation. In locations where mixed-layer depth exceeds 25 m, only a few percent of the particulate carbon supply is sedimented (Hargrave 1975). Exceptions occur, however, when zooplankton are numerous and their grazing produces pellets that settle rapidly. Steele and Baird (1972) and Davies (1975) found that zooplankton fecal pellets predominated material settled in two Scottish lochs. Also, the formation of anoxic bottom water in Tokyo Bay was attributed to the deposition of pellets produced by copepod grazing (Seki et al. 1974).

Seasonal and vertical differences in oxygen uptake by particulate matter settled in Bedford Basin also show that a close coupling exists between organic supply and decomposition rate. During winter and early spring, particulate matter at all depths was refractory to oxidation (Fig. 1). Increased chemical oxidation in material trapped at 60 m could be due to settling of resuspended bottom sediments. After April, however, when microzooplankton volume increased in the water column, through June and July when concentrations of chlorophyll *a* and fecal pellets in deposited material were high (Hargrave and Taguchi 1978), respiration in settled material increased. Material deposited at 20 and 60 m differed in origin, however, since the continued supply of material susceptible to increased respiration and chemical oxidation at 20 m did not appear at 60 m. Correlations of rates of oxygen uptake throughout the year at different depths also show no significant coherence beyond a 20-m depth interval (Table 1). Thus, density differences, deposition of sediments resuspended from different depths, or rapid degradation on sinking during stratification must reduce the supply of oxidizable material below 20 m.

The similarity in absolute rates and seasonal changes in oxygen uptake in Thomas' (1955) and the present study supports the idea that, except during the summer, organic matter settled in traps is resistant to rapid aerobic decomposition. This is not surprising in view of the rates at which particulate organic substrates degrade in water. While initially rapid rates of decomposition may extend over days or weeks for macrophyte debris, algae, and zooplankton held in the laboratory (Harding 1973; Gunnison and Alexander 1975), in all cases degradation proceeds to a final stage where organic matter may still remain (often $> 50\%$) with little further decomposition (Harrison and Mann 1975; Knauer and Ayers 1977). Although degradation of more refractory compounds can occur over time (Gosselink and Kirby 1974), sediments and suspended material collected below the photic zone are usually highly degraded (Matsuyama 1973; Zsolnay 1975). Low rates of oxygen uptake by marine sediments (Waksman and Hotchkiss 1938; Anderson 1939; Hargrave 1972), and low numbers of microorganisms attached to suspended particulate matter (Oláh 1972; Paerl 1973) are characteristics of this refractory material.

The similarity of relationships between respiration and organic content of material settled at all depths in Bedford Basin (Table 2) is further evidence for the resistant nature of deposited material to rapid aerobic degradation. Low rates of respiration per unit organic matter (1–2 mg $O_2 \cdot g\text{-}org^{-1} \cdot h^{-1}$) (Fig. 4), other than during May, are comparable to the lowest rates observed with different substrates from various marine and freshwater locations (Anderson 1939; Hargrave 1972; Gosselink and Kirby 1974; Hargrave and Phillips 1977). This would be expected if decomposition of readily oxidized substrates occurred during collection of settled material (Johnson and Brinkhurst 1971). Bacterial utilization of up to 60% of substrate has been observed over a few weeks (Gosselink and Kirby 1974; Knaeur and Ayers 1977). In other studies material deposited in sedimentation traps, which as in the present study had already undergone some decomposition, was metabolized to a lesser degree (32%) (Seki et al. 1968).

Particulate matter sedimented onto the bottom continues to decompose (both aerobically and anaerobically) and is susceptible to consumption by benthic invertebrates. Some stimulation of benthic metabolism in Bedford Basin would then be expected due to the input of material undergoing more rapid decomposition during early summer (Fig. 2). In addition, egestion of detritus and sediment as feces by invertebrates should lead to a temporary enhancement of oxygen uptake (Hargrave 1976). Seasonal changes in oxygen consumption by undisturbed sediments should reflect the supply and subsequent utilization of oxidizable substrate, if the flux of these materials is important in determining rates of benthic metabolism.

Pamatmat (1977) has reviewed factors that affect oxygen uptake by aquatic benthic communities. He concluded that the supply of oxidizable organic matter was of primary importance. A correlation between annual oxygen uptake by sediments and estimates of particulate carbon supply (Hargrave 1973) supports the idea. Earlier studies also showed that oxygen consumption and temperature were correlated during the year (Hargrave 1969). In the studies compared, however, high temperatures occurred during summer when the supply of freshly produced organic matter is also high. Observations in English rivers (Edwards and Rolley 1965), Puget Sound (Pamatmat and Banse 1969; Pamatmat 1971) and Bedford Basin (Fig. 3) all show a seasonal cycle in total or chemical oxygen uptake which is independent of changes in temperature. The short

time lag between maximum total oxygen uptake and peak chemical oxygen consumption in the present study implies that reduced compounds produced during aerobic respiration are rapidly metabolized.

Rates of total oxygen uptake and respiration by material sedimented in Bedford Basin were increased above minimum values between May and September (Fig. 1). This corresponds to the period when respiration in bottom sediments was also enhanced (Fig. 4) and when the carbon equivalent of sediment respiration corresponded to organic carbon sedimentation (Table 3). Similar efficient utilization of organic matter during the year of deposition has been observed previously (Johnson and Brinkhurst 1971; Davies 1975). The absence of immediate stimulation of benthic metabolism by deposition of material with high chlorophyll *a* content and respiration rate in May (Fig. 2 and 4), on the other hand, must reflect delayed incorporation of freshly deposited phytoplankton in the benthic food web. Such accumulations of undegraded plant pigments in living phytoplankton could account for the appearance of intact algae cells in subsurface sediments (Stockner and Lund 1970). The observations thus support the idea (Pamatmat 1977) that respiration by intact benthic communities provides an integrated not an instantaneous measure of oxidizable organic matter recently supplied to sediments.

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Modified Oxidation/Fermentation Medium for Use in Identification of Bacterial Fish Pathogens

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WALTERS, G. R., AND J. A. PLUMB. 1978. Modified oxidation/fermentation medium for use in identification of bacterial fish pathogens. J. Fish. Res. Board Can. 35: 1629–1630.

A medium, designated glucose motility deep (GMD), was developed to determine motility, oxidation, fermentation, and gas production of gram-negative, cytochrome oxidase positive, bacterial fish pathogens in one culture tube. The medium is intended to replace the current glucose oxidation–fermentation test which requires two tubes and a petrolatum overlay. Isolates of *Aeromonas hydrophila*, *A. salmonicida*, *Pseudomonas fluorescens*, *Vibrio anguillarum*, and *Pasteurella piscicida* were inoculated into GMD. The oxidation–fermentation metabolism, motility, and gas production of each isolate agreed with results obtained using conventional methods.

Key words: bacteriology, bacterial medium, fish disease, fish pathogens, *Aeromonas*, *Pseudomonas*, oxidation/fermentation, identification

WALTERS, G. R., AND J. A. PLUMB. 1978. Modified oxidation/fermentation medium for use in identification of bacterial fish pathogens. J. Fish. Res. Board Can. 35: 1629–1630.

Nous avons mis au point un milieu de culture que nous désignons par le sigle GMD (« glucose motility deep »), permettant de déterminer, dans un tube à culture, la motilité, l'oxydation, la fermentation et la production de gaz de bactéries gramnégatif cytochrome oxydase-positif, pathogènes des poissons. Ce milieu est destiné à remplacer l'actuel essai oxydation–fermentation du glucose nécessitant deux tubes et un enduit de pétrolatum. Nous avons inoculé dans le GMD des isolats d'*Aeromonas hydrophila*, *A. salmonicida*, *Pseudomonas fluorescents*, *Vibrio anguillarum* et *Pasteurella piscicida*. Pour chaque isolat, le métabolisme d'oxydation-fermentation, la motilité et la production de gaz s'accordent avec les résultats obtenus avec les méthodes conventionnelles.

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IDENTIFICATION procedures for gram-negative bacteria isolated from fish have been described by Shotts and Bullock (1975). Some definitive tests are cytochrome oxidase reaction, motility, oxidation and fermentation (O/F) of glucose, and the production of gas from glucose. Using these tests, the major cytochrome oxidase positive pathogens can be differentiated. Rimler–Shotts medium (Shotts and Rimler 1973) was also developed to specifically identify *Aeromonas hydrophila*, a common pathogen of warmwater fishes.

Single tube oxidation fermentation reactions were described by Brown (1974) using the Beckford constricted tube and by Porres and Stanyon (1974) using 10 mL rather than 5 mL of Hugh–Leifson O/F medium. We propose an alternate medium for determining the O/F reaction, gas production, and motility. The medium presently in use is the O/F basal medium of Hugh and Leifson (1953) containing 1% glucose, which has a distinct disadvantage of requiring two test tubes for each organism identified; one tube each for oxidation and fermentation, as well as sterile petrolatum for the overlay. The proposed medium requires no petrolatum overlay and gives oxidation and fermentation readings, gas production, and motility from one tube.

Materials and methods — Glucose motility deep (GMD) medium contains 16 g phenol red broth base (Difco), 10 g glucose, 3 g agar, and 3 g yeast extract/L. The ingredients

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TABLE 1. Results of tests with four gram-negative, cytochrome oxidase positive, bacterial fish pathogens after 24 h in glucose motility deep medium at 25°C.

Species of bacteria	*Aeromonas salmonicida*	*Aeromonas hydrophila*	*Pseudomonas fluorescens*	*Vibrio anguillarum*
No. of isolates tested	13	36	12	6
Percentage oxidative positive[a]	100	100	100[b]	100
Percentage fermentative positive	97	100	0	100
Percentage motility positive	0	100	100	100
Percentage aerogenic positive	0	94	0	100

[a]Percentages based on number of tubes inoculated.
[b]May require 48 h.

are dissolved in deionized water by boiling, pH adjusted to 7.6, and dispensed in 10-mL portions into 16 × 125-mm culture tubes and sterilized at 118°C for 10 min.

Isolates of *Aeromonas hydrophila*, (36), *A. salmonicida* (13), *Pseudomonas fluorescens* (12), *Vibrio anguillarum* (6) and *Pasteurella piscicida* (1), all of which had been isolated from fish, were tested in the GMD medium. Triplicate tubes of GMD were inoculated by stabbing from 24-h trypticase soy broth cultures (Baltimore Biological Laboratory) of each isolate. All tubes were incubated at 25°C and read at 24 and 48 h postinoculation.

Results and discussion — Before inoculation GMD is red (pH 7.6). After inoculation the following changes may take place: oxidation — the top 1 cm of the medium turns yellow from acid production; fermentation — the remainder of the medium turns yellow; motility is indicated by fuzzy outgrowth along the stab line while nonmotile organisms grow only on the stab line; gas production is indicated by bubbles which form in the medium or accumulate at the surface.

Isolates of the five species of bacteria react in GMD almost identically as would be expected in conventional media (Table 1). With the exception of *P. fluorescens*, reactions do not change from 24 to 48 h and the reactions of many active isolates of *A. hydrophila* may be read after 8 h. At 24 h *P. fluorescens* may be more alkaline in the upper 1 cm, but at 48 h this area is acid with the remainder of the tube alkaline. *Pasteurella piscicida* is nonmotile in GMD and ferments the glucose more weakly than *A. salmonicida*. As with all fermentation media, GMD should be resteamed for 3 min and cooled before inoculation if it is not used within 2 d of preparation. However, tightly capped tubes 3 wk old have been used without resteaming with no detectable difference except that oxidative organisms produced acid to a depth of 2 cm rather than 1 cm. Highly aerogenic *A. hydrophila* produced many 1–2 mm diam gas bubbles scattered throughout the medium within 8–12 h in GMD, but after 24 h many of the bubbles had dissipated. Gently shaking the inoculated tube after incubation may be necessary to observe gas production.

GMD has been used by the Southeastern Cooperative Fish Disease Project Diagnostic Laboratory since March 1977 in the identification of fish pathogenic bacteria. In addition to the data in Table 1, GMD was used instead of O/F glucose in identifying 40 isolates of *A. hydrophila*, 16 isolates of *A. salmonicida*, 11 isolates of *Pseudomonas* sp., and 4 isolates of *V. anguillarum*, and all reacted as would be expected in conventional O/F glucose. This medium is effective, easier to use than the standard O/F medium, and reduces the amount of required glassware. Although GMD may prove useful in identification of other bacterial organisms, we can only attest to its value with those pathogenic organisms isolated from fish.

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Numerical Model of the Circulation in an Open Bay

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PETRIE, B., AND K. DRINKWATER. 1978. Numerical model of the circulation in an open bay. J. Fish. Res. Board Can. 35: 1631–1635.

An external alongshore current setting to the east and across the mouth is proposed as the driving mechanism for the measured clockwise circulation in St. Georges Bay, Nova Scotia. A barotropic numerical model of an open bay forced by an alongshore current was able to produce a clockwise gyre in the bay. The model current velocities were in good agreement with the data. The generation, size, and intensity of the gyre required low values of vertical viscosity relative to horizontal viscosity.

Key words: numerical model, bay, gyre, circulation, barotropic, current, coastal

PETRIE, B., AND K. DRINKWATER. 1978. Numerical model of the circulation in an open bay. J. Fish. Res. Board Can. 35: 1631–1635.

Nous émettons l'hypothèse qu'un courant littoral extérieur, en direction de l'est et traversant l'entrée de la baie, est le mécanisme produisant une circulation dans le sens des aiguilles d'une montre mesurée dans la baie St-Georges, Nouvelle-Écosse. Il a été possible à un modèle numérique barotropique d'une baie ouverte entraîné par un courant littoral de produire un tourbillon dans le sens des aiguilles d'une montre dans la baie. Les vitesses de courant du modèle s'accordent bien avec les données. La naissance, la taille et l'intensité du tourbillon ne requièrent que de faibles valeurs de viscosité verticale par rapport à la viscosité horizontale.

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ST. GEORGES BAY, Nova Scotia, shown in Fig. 1 is approximately 30 × 30 km, has a mean depth of about 30 m, and is open at its northern end to the Northumberland Strait and the Gulf of St. Lawrence. In 1974 and 1975 a program of current meter moorings and hydrographic measurements was conducted as part of a study of the fisheries and physical oceanography of the bay. Mooring locations are indicated in Fig. 1.

This note briefly reviews the experimental results that indicate the presence of a mean clockwise circulation in St. Georges Bay, proposes a possible mechanism for driving the gyre, and, lastly, presents the results of a numerical study of a model open bay.

Experimental results — Petrie and Drinkwater (1978) have summarized the main features of the circulation in St. Georges Bay. The average root mean square amplitude ($\simeq$6 cm·s^{-1}) of the mean circulation is comparable to the amplitudes of currents in the tidal and low (periods of 1–8 d) frequency bands. At 8 m a strong clockwise gyre is apparent and is mirrored somewhat at the 20-m level. The flow at 30 m is basically out of the bay. The integrated flow, an average of all data at each station, takes the form of a clockwise circulation.

Generally, the wind stress at the bay was less than 0.1 Pa and correlations between currents and wind stress were low. It is thought that wind is not usually an important driving force for the mean flow in the bay during summer. A wind stress curl large enough to produce the gyre is not expected over such a small bay. It was felt therefore that the gyre may be forced externally by an alongshore current in Northumberland Strait.

Evidence for an alongshore current moving from west to east past the mouth of St. Georges Bay comes from several sources. Farquharson (1959) measured a residual flow at 13 m of about 20 cm·s^{-1} to the southeast over a 12-d period in August at a mooring site in the Northumberland Strait about 90 km west of the bay. Measurements made over a 25-h period at two sites in the entrance of the bay showed "fairly strong" residual currents setting in a northeasterly direction. Lauzier (1965) concluded from surface drift bottle returns that there was a northeasterly flow out of the Northumberland Strait with an approximate mean speed of 7.5 cm·s^{-1}. Returns from surface drift bottles released in St. Georges Bay in 1974 and 1975 (Petrie and Drinkwater 1977a, b) suggest a northeasterly current along the coast of Cape Breton of about 12 cm·s^{-1}. Only 3 of the 152 re-

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FIG. 1. St. Georges Bay, Nova Scotia. Current meter moorings were at Stations 1–8.

turns were located to the west of the bay. Current meter profiles taken by us over a 14-h period on a 9-km section normal to the coast about 10 km to the west of Cape George showed that the upper half (20 m) of the water column between the coast and 4.5 km offshore was moving to the northeast during the entire period. Maximum speeds attained were 50 cm · s^{-1} and did not fall below 10–20 cm · s^{-1}. Farther offshore the flow was weaker but still to the northeast. Tidal currents dominated the water movement near the bottom. All sources indicate a flow from west to east across the mouth of the bay in the upper layers.

Numerical model — Recently Hsueh and Peng (1973) have studied the effect of various driving forces, including an external alongshore current, on the circulation of an open bay. There are two fundamental points at which this work differs from theirs. Firstly, they specified a sinusoidal alongshore current at the mouth of the bay as a boundary condition. Secondly, they discussed only one example of the generation of a gyre in the bay by an alongshore flow and in that case wind complicated the interpretation of the results.

Basic assumptions — The model equations used in this study are similar to those used by Paskausky and Reid (1972). However, in that study the topographic stretching effect on the vorticity was inadvertently omitted in the finite difference formulation. That omission has been rectified in our model and the finite difference form for that term is given in the Appendix. In formulating the model the following assumptions were made:

1. The model was barotropic, hydrostatic, nonlinear, and on an f-plane.

2. A no-slip condition was employed at all solid

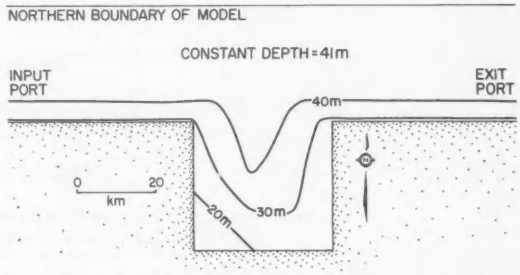

FIG. 2. The model bay with depth contours is shown. Northern boundary of the model is a streamline unaffected by the presence of the bay.

lateral boundaries and a constant horizontal eddy viscosity, A_h, was assumed. The northern free boundary was taken as a streamline, unaffected by the presence of the bay and with zero vorticity.

3. Bottom friction was linear and was matched to an Ekman boundary layer solution of constant vertical eddy viscosity, A_v.

4. The natural bottom topography of the bay was used after some smoothing. The lateral boundaries within the bay were rectangular and the outside "Northumberland Strait" coastline intersected the bay normally. The former assumption closely approximates reality while the latter one, though not quite true, should not affect the qualitative results seriously.

5. The "Northumberland current" entered the input open boundary normally and was required to leave the exit port in the same fashion. The current profile was specified only at the input port and was allowed to evolve downstream according to the governing equations before intersecting the open bay.

The model bay used in the numerical calculations is drawn to scale in Fig. 2. The grid that included the model bay and outside strait was 43 × 23 points with a spacing of 3 km.

A vorticity equation was derived from the momentum equations and has the form:

$$\frac{\partial \zeta}{\partial t} + \nabla \cdot [(f + \zeta)V_h] = A_h \nabla_h^2 \zeta - \sigma \zeta \tag{1}$$

where ζ is the vorticity;
f is the Corliolis parameter;
V_h is a horizontal velocity component;
A_h is the horizontal eddy viscosity; and,
$\sigma = (A_v f/2)^{1/2} D^{-1}$ comes from matching a linear bottom friction term in the momentum equations to an Ekman bottom boundary layer with vertical viscosity A_v. D is the water depth.

The stream function, ψ, satisfying the continuity equation is defined by

$$DU = -\psi_y \quad \text{and} \quad DV = \psi_x \tag{2}$$

where U and V are the eastward and northward com-

ponents of velocity and x and y the east and north coordinates. The vorticity is written as

$$\zeta = \nabla \cdot (D^{-1} \nabla \psi). \tag{3}$$

Details of the derivations and numerical methods were given by Paskausky and Reid (1972) and Paskausky (1971). A very useful discussion was presented by Pearson (1965). Briefly, the equations were solved as follows. Equations (1) and (3) were written in finite difference form using central differencing for both time and space derivatives. A Dufort–Frankel scheme (Smith 1965) was used for the horizontal diffusion term. Equation (1) was time-stepped while equation (3) was solved by successive overrelaxation. The relaxation parameter was 0.40 and the time step varied from 400 to 4000 s depending on the value of A_h. Convergence was determined by monitoring changes in stream function in the model bay. In addition, the total vorticity in the system was calculated as a function of time to ensure that it was constant as the model converged to a steady state.

Nondimensional analysis — Under steady-state conditions in a bay of constant depth the nondimensional vorticity equation may be written as a balance between vorticity advection, horizontal diffusion, and bottom dissipation

$$V \cdot \nabla \zeta = E_h \nabla^2 \zeta - E_v \zeta. \tag{4}$$

The characteristic nondimensional Ekman numbers are

$$E_h = A_h / V_0 L \tag{5}$$

$$E_v = \sigma L / V_0 \tag{6}$$

where V_0 is the characteristic velocity;
and, L is the horizontal length scale which was taken as 30 km, the width of the bay.

The model was run for a bay of constant depth to determine the streamline pattern as a function of the Ekman numbers. For these cases, A_h was varied from 10^2 to 2×10^3 m$^2 \cdot$s^{-1}, A_v from 0 to 10^{-2} m$^2 \cdot$s^{-1}, and the depth was 50 m. Note that σ is depth dependent. The velocity input applied in the model was taken as the solution to the linearized momentum equations for a straight coast and is given in dimensional units by

$$\psi = -U_0 D[y - (A_h/\sigma)^{1/2}(1 - e^{-(\sigma/A_h)^{1/2} y})]. \tag{7}$$

For boundary conditions, the stream function and velocity were taken as zero at the coast, the velocity was constant as $y \to \infty$, and the growing solution was dropped. The results of model runs with various combinations of E_v and E_h are shown in Fig. 3. An "x" indicates that all east–west flow in the bay was in the same direction as the input current. A dot indicates the presence in the bay of any flow in a direction opposite to the input current. The dashed line, intended only as a visual aid, separates the two regimes. Figure 3 indicates that when the vertical term decreases relative to the horizontal term a gyre is formed in the bay.

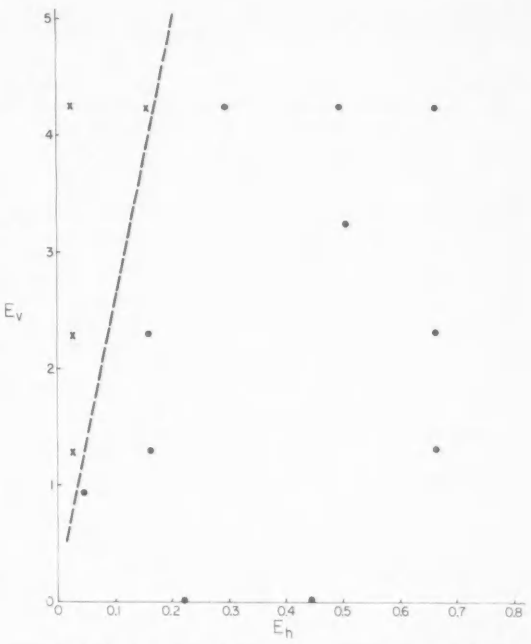

FIG. 3. Results of model runs for the flat-bottomed case and various combinations of vertical and horizontal eddy viscosities are shown. Dot indicates the presence in the bay of any circulation opposing the input current. Flow was unidirectional for the runs marked by an "x."

For small E_v relative to E_h, the primary balance must be between vorticity advection and horizontal diffusion. The formation of a gyre in the bay effectively increases the magnitude of the diffusion term enabling this balance to hold. In fact, the most intense and largest gyres were obtained for the two cases in Fig. 3 for which $E_v = 0$. Ideally, in the nondimensional analysis, the formation of the gyre in the model bay should correspond to $E_v/E_h \ll 1$. However, from Fig. 3 it is apparent that this is not so. It appears that the choice of the bay width as the horizontal scale of motion was not appropriate. Note from equations (5) and (6) that reducing the scale by a factor of 2 increases E_h relative to E_v by four times.

Choice of friction and input velocity — In numerical schemes the choice of friction often dictates the results that can be obtained. This was true of the numerical model presented here and made obvious in the last section. In the numerical experiments, we concentrated our efforts on values of A_h in the range 10^2 m$^2 \cdot$s^{-1} and 10^3 m$^2 \cdot$s^{-1}. Since the nondimensional analysis showed the most intense gyre to form with the vertical eddy viscosity zero, we attempted diagnostic calculations using that value. Currents computed with these coefficients compare well with the data.

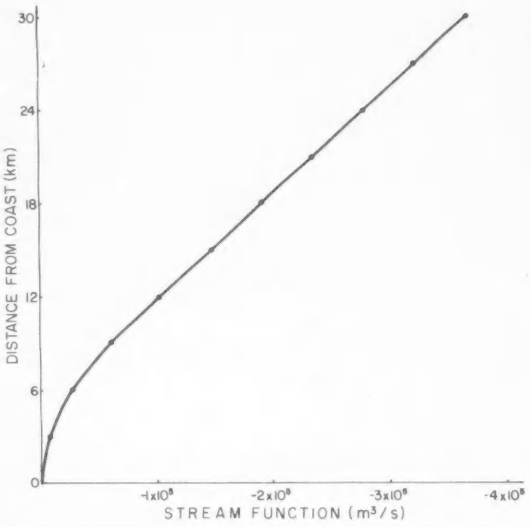

FIG. 4. The input port stream function for all model runs is plotted as a function of distance from the coast.

The stream function for the input port is shown as a function of distance from the coast in Fig. 4. The current speed 3 km from the coast was 14 cm·s^{-1} and at 30 km was 35 cm·s^{-1}. These currents are about the same strength as have been observed in Northumberland Strait.

Model results — The streamline patterns are shown in Fig. 5A and B for $A_h = 10^3$ and 10^2 m^2·s^{-1}, respectively. The first case produced a nearly symmetric gyre in the bay with flows of 9 cm·s^{-1} across the mouth and currents of 1.5 cm·s^{-1} into the bay on the eastern side and 1.2 cm·s^{-1} out of the bay on the western side. With $A_h = 10^2$ m^2·s^{-1} distortion of the gyre becomes evident. The flow into the bay has been confined to a smaller region on the eastern side and inflow velocities have intensified to 3 cm·s^{-1}. The outflow has broadened and has remained at 1.2 cm·s^{-1} near the western coast. The asymmetry of the circulation is caused by nonlinear effects (as in Pearson 1965) and topographic effects. Within the southern portion of the bay westward flows are about 0.8 cm·s^{-1}. These values compare well with current meter results where depth-integrated flows were about 8 cm·s^{-1} across the mouth, 1.6 cm·s^{-1} out of the bay on the western side, and 4.4 cm·s^{-1} into the bay on the eastern side. Velocities in the southern part of the bay were about 2.4 cm·s^{-1}.

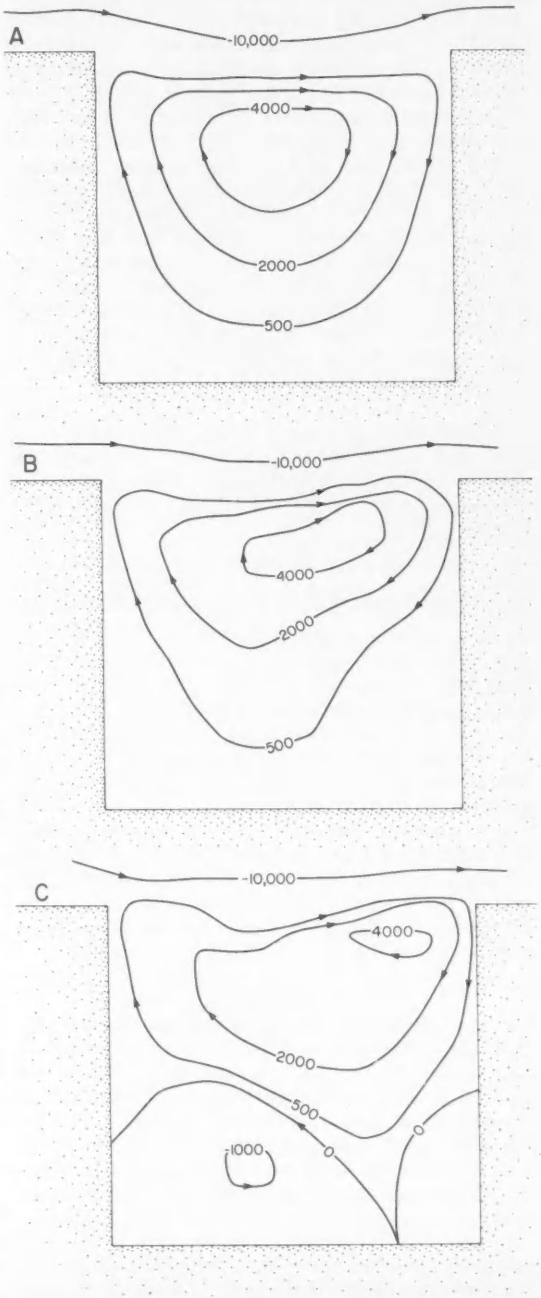

FIG. 5. A) The steady-state stream function for the model open bay is shown for the case $A_v = 0$, $A_h = 1000$ m^2·s^{-1}. Contours are in units of cubic metres per second. B) The steady-state stream function for the model open bay is shown for the case $A_v = 0$, $A_h = 100$ m^2·s^{-1}. Contours are in units of cubic metres per second. C) The steady-state stream function for the model open bay is shown for the case $A_v = 0$, $A_h = 25$ m^2·s^{-1}. Contours are in units of cubic metres per second.

Several runs yielding interesting results were made at lower values of horizontal eddy viscosity. An example is shown in Fig. 5C with $A_h = 25\ m^2 \cdot s^{-1}$. The asymmetry of the gyre has increased and another one with opposing circulation has appeared in the southern end of the bay. Westward flows in the center have intensified. The appearance of the second gyre maintained the balance between advection and diffusion of vorticity while lowering A_h. Further reduction of A_h would necessitate a smaller grid size to resolve the increasingly smaller eddies. Such a refinement would not be fruitful given the assumptions that have already gone into the model.

Discussion — Frictional terms that are not well understood have played a prominent role in the present model. Consideration of equation (1) will show why this is so. In the absence of friction and topography relative vorticity is conserved along streamlines. This fact coupled with the coast being a streamline would prohibit the formation of a gyre. The imposition of friction, under appropriate conditions, allowed gyres to form similar to those found by Moffatt (1964).

The model presented can, under the restrictions indicated, produce barotropic currents in the bay in good agreement with observations. However, the mean velocity structure and the hydrography (Petrie and Drinkwater 1978) of the bay were obviously baroclinic. A logical and useful extension of the model would be to two layers. Another important step would be to obtain current measurements in the Northumberland Strait of similar concentrations and duration as those in the bay to improve the boundary conditions.

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Appendix

Finite Difference Form

The formulation used in this paper for the second term in equation (1) was

$$\frac{\Delta t}{2\Delta S^2}[(f + \zeta^n_{j+1,k})(\psi^n_{j+1,k-1} - \psi^n_{j+1,k+1})/D_{j+1,k} - (f + \zeta^n_{j-1,k})(\psi^n_{j-1,k-1} - \psi^n_{j-1,k+1})/$$
$$D_{j-1,k} + (f + \zeta^n_{j,k+1})(\psi^n_{j+1,k+1} - \psi^n_{j-1,k+1})/D_{j,k+1} - (f + \zeta^n_{j,k-1})(\psi^n_{j+1,k-1} - \psi^n_{j-1,k-1})/D_{j,k-1}]$$

Separation of Two Dissolved Reactive Phosphorus Fractions in Lakewater

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DOWNES, M. T., AND H. W. PAERL. 1978. Separation of two dissolved reactive phosphorus fractions in lakewater. J. Fish. Res. Board Can. 35: 1636–1639.

A method for the separation of two dissolved reactive phosphorus (DRP) fractions in unconcentrated lakewater is described. A reactive high molecular weight phosphorus (RHMW-P) fraction has been found in all waters studied and a second fraction, corresponding to orthophosphate (PO_4-P) is frequently detected. The hydrolysis of RHMW-P to PO_4-P by acid in the analytical reagents is shown to be the most likely reason for its determination as DRP.

Key words: freshwater analysis, reactive phosphorus, orthophosphate, molybdenum blue method, gel filtration

DOWNES, M. T., AND H. W. PAERL. 1978. Separation of two dissolved reactive phosphorus fractions in lakewater. J. Fish. Res. Board Can. 35: 1636–1639.

Nous décrivons une méthode de séparation de deux fractions de phosphore réactif (DRP) dans de l'eau de lac non concentrée. Nous avons trouvé une fraction de phosphore réactif de poids moléculaire élevé (RHMW-P) dans toutes les eaux examinées et une seconde fraction, correspondant à l'orthophosphate (PO_4-P), a été fréquemment détectée. L'hydrolyse de RHMW-P en PO_4-P par l'acide des réactifs analytiques est la cause la plus probable de son identification comme DRP.

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THE validity of the molybdenum blue technique for measuring dissolved orthophosphate in aquatic ecosystems has been questioned. Kuenzler and Ketchum (1962) and Rigler (1966 and 1968) have suggested that this method exaggerated the concentration of dissolved orthophosphate by 10–100 fold. Rigler (1968) showed that an anion exchange resin was unable to remove all dissolved reactive phosphorus (DRP) from a filtered lakewater sample even though the same resin retained 96% of a ^{32}P-labeled orthophosphate (PO_4-P) spike. The DRP passing through the resin represented 26.5% of the DRP in the original sample and he suggested that the DRP in the effluent could be associated with large organic molecules which failed to penetrate the resin pores, and are therefore less efficiently removed than PO_4-P. If some of these molecules were hydrolyzed during the subsequent analysis they would be measured as DRP. A similar effect was noted during experiments with GF/C filtrates of water from Lake Tutaeinanga which is situated in the agricultural central plateau region of the North Island of New Zealand. These filtrates contained 37 mg $P \cdot m^{-3}$ of DRP but only 22% of this was removed by passing the filtrate through Amberlite IRA 402 anion exchange resin. The same resin removed 83% of the phosphorus from a 40 mg $P \cdot m^{-3}$ standard PO_4-P solution. If Rigler's suggestion is correct it should be possible to separate DRP in lakewater into two or more fractions according to their molecular size. The following describes a technique for separating unconcentrated lakewater DRP and its application to the examination of the DRP distribution in several lakes in the North Island of New Zealand.

Materials and methods — Two techniques which separate solutes by their molecular size are ultrafiltration through either membranes or gels. The former technique was considered to be unsatisfactory when dealing with colloidal forms of phosphorus, since a high percentage of particles smaller than the membrane pores are retained on the membrane by van de Waal's forces, entrapment in the pores, and by sorption to previously retained particles (Olsen 1967). Sephadex gels, however, have been successfully used to separate ^{32}P-labeled compounds in lakewater (Lean 1973). G-25 (fractionation range of 100–5000 MW) coarse gel was selected as the most suitable fractionation medium since it was characterized by fast flow rates and good separation

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between PO_4-P and higher molecular weight reactive phosphorus compounds.

A column of G25-150 gel, 26 cm long and 2 cm in diameter was used with 0.2% sodium chloride and 0.03% sodium azide as the eluent. Disks of Whatman GF/A paper were placed at the top and bottom of the gel column to minimize disturbance of the beads. The void volume of the column, determined with dextran blue, was 25 mL. Flow rates were adjusted to about 2 mL·min^{-1} and were measured at the beginning and the end of each run and, if different, averaged. No differences exceeding 10% of initial flow rates were detected. The effluent from the column was continuously monitored for DRP using Technicon Auto Analyzer II equipment sampling at 1 mL·min^{-1}. The analytical manifold was capable of detecting 1 mg PO_4-P·m^{-3} and was protected against arsenate interference by the addition of a thiosulphate–metabisulphite solution before addition of the color reagent. (M. T. Downes unpublished data) The color reagent was similar to that of Strickland and Parsons (1968), but contained a higher concentration of potassium antimonyl tartrate to overcome the inhibitory effect of the reductant on the color development. The continuous monitoring of effluent gives greatly improved resolution and sensitivity over discrete fraction collection techniques, especially at low eluent flow rates. The colorimeter output was fed to a continuous trace chart recorder. Using this system the time required to run a complete chromatogram (elution time + analysis time) was 32 min. For each run the eluent reservoir was disconnected from the top of the column and the tap at the bottom of the column closed. The eluent on the top of the gel (10 mL) was withdrawn through a syringe. A 5-mL sample was then pipetted onto the top of the gel and the bottom tap opened allowing the sample to soak into the top of the column but not allowing the top of the gel to run dry. The eluent was then returned to the top of the column and the eluent reservoir reconnected starting the elution.

A freshly prepared gel appeared to have active sites which irreversibly absorbed some high molecular weight fractions of phosphorus. This could be overcome by carrying out elutions of several 5-mL aliquots of sample until reproducable chromatograms were obtained at which time near 100% recovery of added phosphorus was consistently obtained. Alternatively, aliquots of a sodium phytate [$C_6H_6(O\cdot PO_3Na_2)_6$] solution containing 200 mg P·m^{-3} were used for this purpose. In this case the column effluent was sampled at 1.6 mL·min^{-1}, segmented with air (0.8 mL·min^{-1}) mixed with 10% sodium perchlorate solution in 1 N H_2SO_4 (1 mL·min^{-1}) and passed through 3 m of 3 mm ID silica tubing, coiled around a 1 kW "Hanovia" mercury discharge lamp. After passing through the coil the stream was resampled and analysed for PO_4-P using the same manifold referred to above. At least 95% of the P in sodium phytate and 100% of the P in sodium glycerophosphate was converted to PO_4-P by this method. This technique was also used for estimating dissolved unreactive phosphorus (DUP) in lakewater. About 20 mL of 200 mg P·m^{-3} sodium phytate was usually sufficient to condition a new gel to give 100% recovery. Azide was omitted from the eluent when using the DUP procedure as it was found to interfere with the UV digestion step.

Water samples were collected in litre acid-washed polyethylene bottles and filtered through acid washed GF/C papers within 2 h of collection. Analyses and chromatograms were run on the day of collection, with occasional samples being stored at 4°C overnight and rerun the next day. All lakes in this study were small, eutrophic, and had predominantly agricultural catchments. Diatoms and blue-green algae were the dominant phytoplankton species.

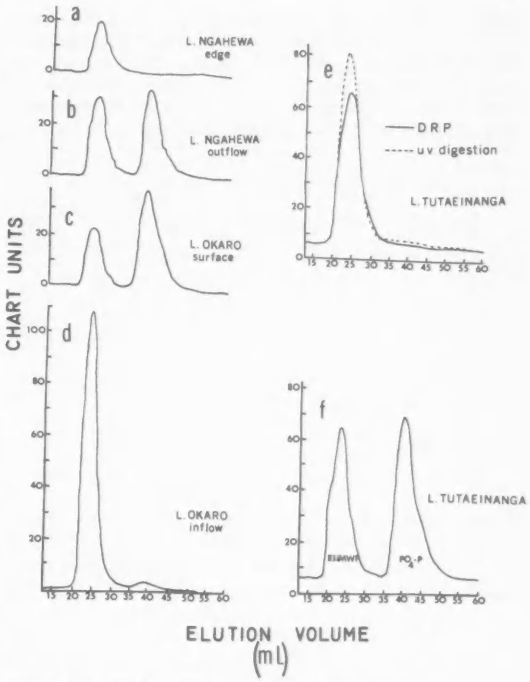

FIG. 1. Sephadex fractionations of the filtrates of several natural waters from the North Island of New Zealand. a, b, c, d) DRP analyses; e) DRP and TDP analyses; f) Filtrate from e + PO_4-P analyzed for DRP.

Results and discussion — All water samples examined contained a reactive high molecular weight phosphorus component (RHMW-P) which eluted at the gel void volume, indicating a molecular weight of >5000 (Fig. 1). The only other DRP component resolved was eluted at the same volume as PO_4-P from a standard orthophosphate solution which was used to calibrate the column. In all waters examined the RHMW-P component represented a substantial fraction of the total DRP ranging from 13 to 100%. Any DUP in the filtrates always coincided with first peak eluted (Fig 1e). The results are summarized in Table 1.

Rigler (1968) in experiments using hydrous zirconium oxide (HZO) to strip [^{32}P]PO_4-P from lakewater, found that it did so, but less efficiently than from distilled water. He suggested the possibility of a compound in lakewater that exchanges rapidly with dissolved PO_4-P. To test for this reaction, carrier free ^{32}P-labeled PO_4-P was added to the filtrate from Lake Tutaeinanga which contained no detectable orthophosphate. Samples of this amended filtrate were then

TABLE 1. The phosphorus distribution of GF/C filtered waters in $mg \cdot m^{-3}$ P. DUP is the additional DRP response when the sample undergoes UV digestion. DRP recovery was calculated from the areas of the chromatograph peaks and related to the amount of DRP put onto the Sephadex column.

Sample	DRP				
	Total	RHMW-P	PO_4-P	Recovery (%)	DUP
L. Ngahewa (edge)	24	17	7	101	5
L. Ngahewa (outflow)	56	25	31	99	12
L. Okaro (surface)	50	7	44	103	11
L. Okaro (inflow)	73	72	3	103	11
L. Tutaeinanga	37	39	1	103	23

chromatographed 3 and 24 h after ^{32}P additions. Fractions of column effluent were collected on plastic caps which were then air dried at 60°C and counted on a Philips PW4633 gas flow planchet counter. The chromatograms from this experiment (Fig. 2) showed only a slow accumulation of radioactivity in the RHMW-P fraction with time, indicating that this reaction was not significant in this lake. After 3 h 95% of the ^{32}P added to the Sephadex column was recovered in the elutions while after 24 h 92% of the ^{32}P added was recovered. The slight discrepancy appeared to be due to some form of ^{32}P being irreversibly bound to the gel. We also spiked an identical filtrate with 60 $mg \cdot m^{-3}$ PO_4-P to test whether increasing PO_4-P levels would cause more RHMW-P to be formed. No significant exchange was observed with 30 min (Fig. 1f) when Sephadex separation was conducted on spiked filtrate. The ability of RHMW-P to maintain its integrity and constant concentration in the face of orthophosphate spikes followed by storage indicates that phosphate must be a firmly bound component of RHMW-P and that fresh sources of PO_4-P are not rapidly "harvested" by a colloidal component of lakewater.

In addition to the molecular separation experiments discussed here we have only few data pointing to the chemical nature of RHMW-P. Lakes which contain RHMW-P are located in agricultural catchments supporting dairy farms and grasslands fertilized with superphosphate (P_2O_5). Lake inputs often contain organic wastes and organic soil leachate containing RHMW-P. We suspect that a majority of the RHMW-P in lakewater is organically-bound since UV oxidation converts virtually all the RHMW-P to free PO_4. However, the possibility of FeP and CaP polymers and organic–inorganic complexes acting as RHMW-P cannot be discounted at present.

To test the hypothesis that observed overestimation of orthophosphate in lakewaters was due to the hydrolysis of RHMW-P by the activity of the DRP reagents, the filtrate from Lake Tutaeinanga was also analyzed by the "6-s" phosphorus method of Chamberlain and Shapiro (1969). This method is based on the fact that the rate of reduction of molybdophosphoric acid to molybdenum blue by stannous chloride is rapid at low acidity (0.2 N H_2SO_4) but completely inhibited in 1.8 N H_2SO_4. The molybdenum blue color was allowed to develop at low acidity for 6 s, after which acid was added to stop the reaction. About 75% of the ultimate PO_4-P color (6 min) is developed during this period but interference from PO_4-P produced by hydrolysis is greatly reduced. When this method was applied to the Lake Tutaeinanga filtrate, 6.5% of the color was produced when compared with that at 6 min, indicating that the hydrolysis of RHMW-P takes much longer than 6 s.

We have demonstrated the presence in lakewater, of a component (RHMW-P), other than orthophosphate, which responds to the commonly used molybdenum blue

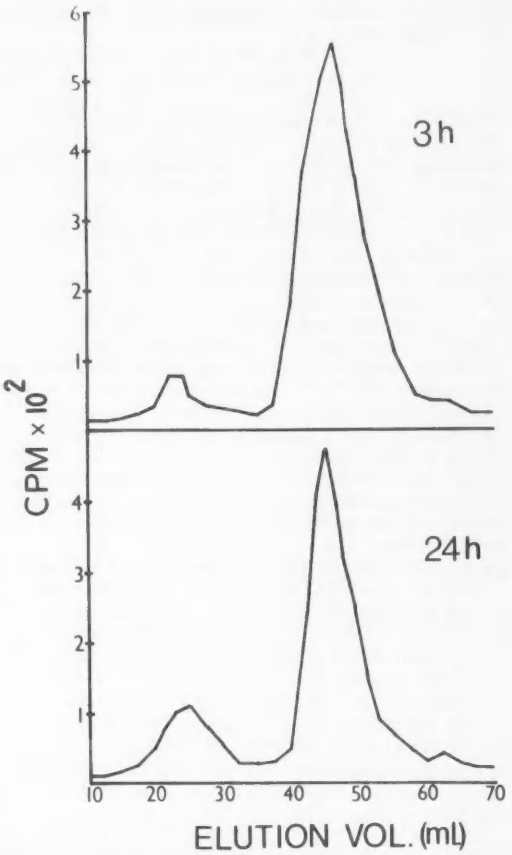

FIG. 2. The distribution of ^{32}P added to Lake Tutaeinanga filtrate as PO_4-P after standing for 3 and 24 h.

methods. It appears most likely that hydrolysis of this fraction to orthophosphate by acid in the reagents is responsible for the overestimation of PO_4-P. Sephadex fractionation studies indicate that RHMW-P has an apparent molecular weight >5000 and only 22% of it is removed by passing lakewater through an anion exchange resin. The properties of RHMW-P are consistent with those hypothesized by Rigler (1968), including failure of HZO to remove SRP while it removed [^{32}P] PO_4-P from lakewater, and the lower values of SRP after separation of inorganic and organic P on HZO columns. The potential biological availability of RHMW-P is discussed in a further paper (Paerl and Downes 1978).

The technique described should also be useful in differentiating the various associations of other nutrients with high molecular weight compounds in natural waters and some preliminary work on nitrogen and iron has already been completed. With regards to phosphorus fractionation, our surveys are at present restricted to lakes having analytically-measurable quantities of reactive P (>10 mg P·m^{-3}) available for Sephadex fractionation. Similar difficulties as discussed above may exist in defining reactive P at the <1 mg P·m^{-3} level.

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Biological Availability of Low Versus High Molecular Weight Reactive Phosphorus

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PAERL, H. W., AND M. T. DOWNES. 1978. Biological availability of low versus high molecular weight reactive phosphorus. J. Fish. Res. Board Can. 35: 1639–1643.

When equivalent concentrations of reactive high molecular weight phosphorus (RHMW-P > 5000) and free orthophosphate (PO_4-P) from Lake Tutaeinanga, New Zealand, were added to P-starved *Chlorella* cultures, free PO_4 showed a faster growth response within 48 h than RHMW-P. Algal preference for PO_4 over RHMW-P could also be shown by (^{32}P)PO_4 turnover experiments. After 96 h both fractions showed good growth yields. Analyses on culture filtrates indicated that all forms of reactive P had been removed. This demonstrates that RHMW-P, which reacts with "reactive P" reagents, can eventually be utilized.

Key words: reactive phosphorus, orthophosphate, algae, *Chlorella*, growth, bioassay

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Quand on ajoute des concentrations équivalentes de phosphore réactif de poids moléculaire élevé (RHMW-P > 5 000) et d'orthophosphate libre (PO_4-P) provenant du lac Tutaeinanga, Nouvelle-Zélande, à des cultures de *Chlorella* manquant de P, le PO_4 libre donne une réaction de croissance plus rapide en dedans de 48 h que le RHMW-P. On peut démontrer également la préférence des algues à l'endroit du PO_4 par rapport au RHMW-P à l'aide d'expériences de renouvellement de $(^{32}P)PO_4$. Après 96 h, les deux fractions montrent de bons rendements en croissance. Les analyses des filtrats de cultures indiquent que toutes les formes de P réactif ont été enlevées. Ceci démontre que le RHMW-P qui réagit avec les réactifs à « P réactif » peut éventuellement être utilisé.

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STUDIES of $(^{32}P)PO_4$ turnover in freshwater have indicated that the true PO_4 pool was much smaller than that determined by analytical methods (Rigler 1956; Lean 1973). Rigler (1968) suggested that hydrolysis of organically bound PO_4 by acid molybdate might be a source of overestimation. Although Chamberlain and Shapiro (1969) felt hydrolysis was minimal, we have shown that the "reactive pool" as measured by Murphy and Riley's (1962) method, modified by Strickland and Parsons (1968), can indeed significantly overestimate free PO_4 concentrations (Downes and Paerl 1978).

In this study the short-term (within several hours) turnover of $(^{32}P)PO_4$ was comparable between lakewaters showing high and low proportions of this "reactive P" present as free PO_4. Coupled with this, the long-term biological availability of both reactive high molecular weight P (RHMW-P) and free PO_4 was tested by inoculating P-starved *Chlorella* cultures with each respective P fraction.

Materials and methods — We demonstrated in an earlier study (Downes and Paerl 1978) that in Lake Tutaeinanga, New Zealand, out of 41 mg·m^{-3} total reactive P only 0.5 mg·m^{-3} P was free PO_4. In contrast, out of 50 mg·m^{-3} total reactive P in Lake Okaro 44 mg·m^{-3} was free PO_4. Each lake contained similar quantities of total reactive P. To see if these large differences in free PO_4 would have an effect on respective PO_4 turnover rates, trace quantities of $^{32}PO_4$ (as phosphoric acid) were added. Turnover times were obtained as described by Rigler (1956) and Lean (1973). Following $(^{32}P)PO_4$ introduction, the radioactivity remaining in evaporated H.A. Millipore (0.45 μm porosity) filtrate was assayed by a Philips PW 4633 gas flow low-level planchette geiger counter. Formalin (1% vol/vol) treated lakewater and H.A. Millipore filtrate control samples were run in parallel as a check on abiotic ^{32}P adsorption and colloidal ^{32}P formation.

Since reactive P in Lake Tutaeinanga was virtually confined to the RHMW-P fraction, it was possible to test biological reactivity of RHMW-P alone. P-starved *Chlorella* spp. initially grown on Gorham's medium (Gorham et al. 1964) free of P were given equivalent amounts (10 mg P·m^{-3}) of RHMW-P (from Lake Tutaeinanga) or PO_4 as $NaHPO_4$ in quadruplicate 100-mL bioassays. Control bioassays, having no additions, were run in parallel in order to check for possible growth inhibition by Lake Tutaeinanga water. A fourth set of bioassays contained both 5 mg P·m^{-3} of RHMW-P and 5 mg P·m^{-3} of PO_4.

Growth response was measured by ATP content (Holm-Hansen and Booth 1966) of *Chlorella*, incorporation of ^{14}C added as bicarbonate (Goldman and Carter 1965), and microscopic counts (Paerl 1978). All bioassays were grown in 125-mL Erlenmeyer flasks on a shaker table at 1300 lx constant illumination. They were subsampled 48 and 96 h after P additions.

Results and discussion — Although total reactive P levels were similar in lakes Okaro and Tutaeinanga on June 10, respective PO_4 turnover times varied substantially. Lake Okaro showed no significant turnover while Lake Tutaeinanga showed a turnover time of 3.7 h (Table 1). In addition to providing information on PO_4 pool size, turnover rates are also dependent on other variables. Among these are temperature, light, and microbial biomass. Temperature and light regimes were excluded as variables by holding them constant during all turnover experiments. Microbial biomass, which can have profound effects on PO_4 demand, was approximated by both ATP assays and microscopic counts. Multiplying cellular ATP content by 250 as an estimate of biomass carbon (Holm-Hansen 1970), we obtained 1150 mg C·m^{-3} for Lake Okaro and 1075 mg C·m^{-3} for Lake Tutaeinanga. Conversion of cell counts to biomass by a cell volume to carbon regression formulated by Mullin et al. (1966) yielded 1020 mg C·m^{-3} and 950 mg C·m^{-3}, respectively. Thus microbial biomass showed little difference between lakes.

TABLE 1. Dissolved reactive phosphorus (DRP) and phosphate (PO_4) concentrations in Lake Okaro and Lake Tutaeinanga waters as determined by Sephadex fractionation followed by autoanalysis. Turnover times of $(^{32}P)PO_4$ were determined on each sample. ND indicates no detectable turnover.

Sample – Date	mg P·m^{-3} DRP	mg P·m^{-3} PO_4	Turnover time (h)
L. Okaro, June 10	50	44	ND
L. Tutaeinanga, June 10	41	0.5	3.7
L. Okaro, July 14	59	47	ND
L. Tutaeinanga, July 14	35	7	19.8

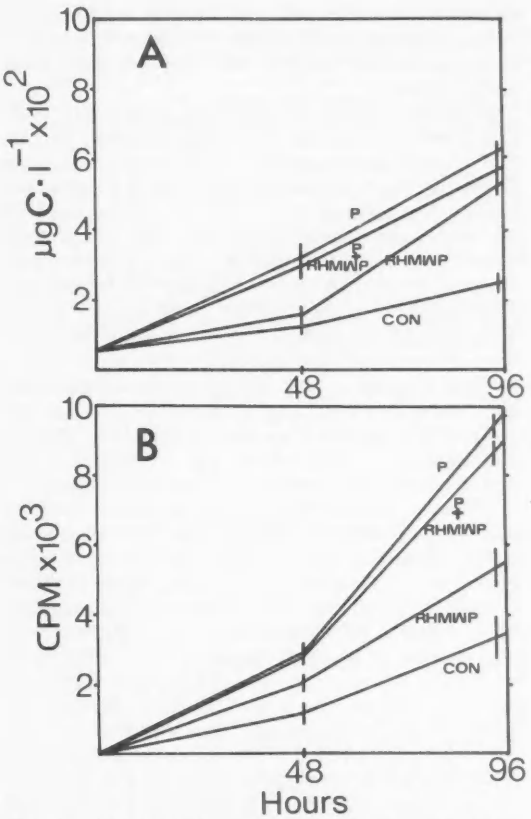

FIG. 1. A) Magnitude of *Chlorella* biomass production as cellular carbon (estimated by ATP content × 250) in response to 10 mg P·m^{-3} of orthophosphate (P), reactive high molecular weight phosphorus (RHMWP), and a combination of both forms. Control bioassays received no additions. Error bars indicate variability among quadruplicate flasks used for each addition; B) Stimulation of *Chlorella* [^{14}C]CO_2 incorporation in response to phosphorus additions identical to those given in Fig. 2A.

Differences in turnover times appeared to reflect contrasting levels of free PO_4 determined by Sephadex fractionation of the lakewater samples. On June 10 Lake Okaro, having approximately 88% of its reactive P as PO_4 had a relatively large PO_4 pool, and accordingly, no detectable turnover within 4 h. Lake Tutaeinanga, however, having virtually all of its reactive P as RHMW-P, revealed a much shorter turnover time.

When turnover experiments were performed on samples taken July 14, turnover times showed a dramatic increase for Lake Tutaeinanga, while Lake Okaro water showed results similar to June 10 (Table 1). Analysis of reactive P pools following Sephadex fractionation revealed that 80% of the reactive P present in Lake Okaro water was free PO_4, while in Lake Tutaeinanga 20% of the reactive P was PO_4. This was a sharp contrast to June 10 when only 1.3% of the reactive P was present as PO_4 in Lake Tutaeinanga. It appeared that the turnover experiments and Sephadex separation complemented each other in demonstrating the reactivity and relative contribution of a free PO_4 pool to the total dissolved reactive P pool. Generally, when small proportions of free PO_4 were present faster turnover rates were recorded.

TABLE 2. Response of P-starved *Chlorella*, as cell numbers, to 10 mg P·m^{-3} additions as PO_4, RHMW-P + PO_4, and RHMW-P. Control cultures received no P additions.

Addition	Cells·mL^{-1} × 10^3 48 h	96 h
Control (no additions)	158	175
10 mg·m^{-3} P as PO_4^{3-}	210	285
5 mg·m^{-3} P as PO_4^{3-} + 5 mg·m^{-3} P as RHMW-P	178	255
10 mg·m^{-3} P as RHMW-P	162	269

TABLE 3. Examination of total reactive P in GF/C filtrate from *Chlorella* bioassays incubated with various forms of reactive P. In all cases *Chlorella* was able to remove these reactive P fractions within 96 h. Total reactive P levels added were analyzed at the start of bioassays (0 incubation time). In a control experiment RHMW-P was added to *Chlorella*-free culture filtrate and incubated for 96 h.

Addition	Incubation time (h)	mg reactive P·m^{-3}
RHMW-P	0	10.2
RHMW-P	96	0.3
PO_4	0	10.3
PO_4	96	0.2
RHMW-P + PO_4	0	10.0
RHMW-P + PO_4	96	0.3
RHMW-P (−) *Chlorella*	0	10.1
RHMW-P (−) *Chlorella*	96	9.8

All bioassay parameters indicated that free PO_4 had a more immediate effect on stimulating *Chlorella* growth than equivalent amounts of RHMW-P (Fig. 1A, B; Table 2). A combination of both reactive forms yielded intermediate results. Faster free PO_4 stimulation did not appear to be due to growth inhibition by RHMW-P fractions, since RHMW-P alone showed significant stimulation over control (no additions) cultures. After 96 h, however, both free PO_4 and RHMW-P showed significant growth over controls. It appeared that although RHMW-P was less available in short-term incubations, this fraction could eventually be utilized to the same extent as free PO_4. Analysis of the filtrate from 96-h bioassays also indicated that all forms of added reactive P were completely utilized (Table 3). The utilization was biologically mediated since RHMW-P added to the medium free of *Chlorella* followed by a 96-h incubation showed unchanged final reactive P

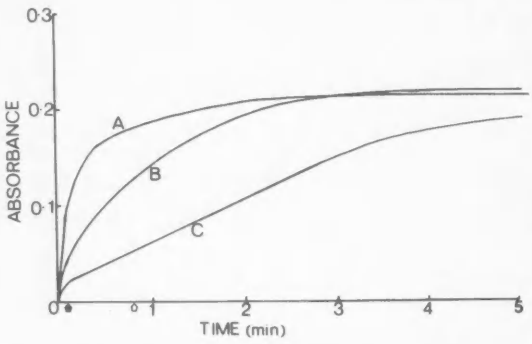

FIG. 2. Spectrophotometric monitoring of color development (absorbance at 698 nm) when 6-s phosphorus reagents were used: A) A 20 mg $P \cdot m^{-3}$ orthophosphate standard; B) Lake Tutaeinanga water (diluted to 21 mg $P \cdot m^{-3}$) of which 16% is orthophosphate and 84% RHMWP; C) Lake Tutaeinanga water (diluted to 18.5 mg $P \cdot m^{-3}$) of which <1% is orthophosphate and >99% is RHMWP. All absorbance values were corrected for reagent blanks. The 6-s phosphorus values (dark arrow) were obtained by stopping the reaction as prescribed by Chamberlain and Shapiro (1969). After 45 s (white arrow) which was the time allotted for mixing reagents and samples and filling a cuvette, color development was monitored continuously. The values between 6 and 45 s were extrapolated using independently derived absorbance values and slopes of respective reaction rates.

levels (Table 3). In more recent experiments the appearance of alkaline phosphatase activity in P-starved *Chlorella* cultures receiving RHMW-P additions has provided additional evidence that this fraction was biologically converted to available P. Cultures receiving PO_4 alone failed to show similar levels of alkaline phosphatase activity (H. W. Paerl unpublished data).

Our results indicate that *Chlorella* will preferentially utilize free PO_4 over RHMW-P, but given enough time in the absence of free PO_4, RHMW-P can be utilized as well. These bioassay results aid in explaining why turnover times of several hours instead of a few minutes were recorded in Lake Tutaeinanga. A turnover time of 3.7 h for a eutrophic lake having such a small pool of free PO_4 is substantially longer than 5–15 min turnover times published for Heart Lake, Canada (Lean 1973), which is comparable in trophic status. Our bioassay results have shown that PO_4 is derived from both PO_4 and RHMW-P pools. This constitutes an appreciable total reactive P pool. The overall effect would be longer turnover times than could be predicted from the very small PO_4 pool alone.

Both bioassay and turnover experiments agree that RHMW-P in Lake Tutaeinanga, which is included as "reactive P" in the Murphy and Riley analysis, can in due time be biologically available. To what extent these findings hold true for diverse lakes is not known. If, however, variability in degrees of short- and long-term biological availability between free PO_4 and RHMW-P occurs, serious discrepancies between reactive P as measured by this method and true biological availability may exist.

In earlier attempts at separating biologically available from total reactive P, Chamberlain and Shapiro (1969) used the 6-s method, whereby molybdate was allowed to react with samples for only 6 s with acidic stannous chloride as a reductant. We performed both 6-s and 6-min determinations on Lake Tutaeinanga water. Dramatic differences in reactive P yields were observed (Fig. 2). After a 6-s exposure to the reagents only one tenth of the P found to be reactive by the Murphy and Riley method was accounted for. However, when the reagents were allowed to react for at least 5 min we obtained a yield similar to the Murhpy and Riley method. Since bioassays demonstrated that virtually all the reactive P as determined by the Murphy and Riley method was utilized, the 6-s method in this case seriously underestimated biologically available P.

We have shown variability in agreement between chemically-determined reactive P and biological availability. Generally, the standard Murphy and Riley method tends to overestimate the most readily available form of P, namely free PO_4. These results substantiate Rigler's earlier contention, based on $(^{32}P)PO_4$ turnover kinetics, that chemically-determined PO_4 levels tend to overestimate free PO_4 (1956). The kinetics of $(^{32}P)PO_4$ turnover are complicated by the fact that RHMW-P can be biologically utilized as well, but at a slower rate than free PO_4. The utilization of RHMW-P in the presence of a relatively small free PO_4 pool can lead to longer turnover times than might be expected from specific chemical measurements. Availability of free PO_4 vs. RHMW-P to algae will need to be surveyed in a range of lakes varying in trophic status before it can be concluded which reactive P method most consistently approximates biologically available P.

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Ammonia Production Rates of *Artemia salina* Under Various Culture Conditions

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MOFFETT, W. L., AND W. S. FISHER. 1978. Ammonia production rates of *Artemia salina* under various culture conditions. J. Fish. Res. Board Can. 35: 1643–1648.

Artemia salina are used as a live food in the cultivation of several Crustacea and their metabolites add to the metabolites of the cultured species. Because it is toxic, ammonia was monitored over 7-d periods while *A. salina* nauplii and adults were held in a variety of culture conditions. Ammonia production increased with increasing temperature between 15–25°C according to the relationship

$$NH_3 + NH_4^+ \text{ (mg/g dry wt per day)} = 0.646\ (°C - 10.3).$$

Production of ammonia by nauplii was density dependent. No change in ammonia production was shown by adults with alteration of density (200–2000 *A. salina*/L), salinity (10–50‰), or pH (7.0–9.0), or when fed twice daily with 50 000–100 000 cells *Platymonas* sp./mL. *Artemia salina* fed ad lib. to cultured experimental lobsters would contribute about 46% of the total ammonia in the culture system.

Key words: Artemia, aquaculture, ammonia, metabolism, excretion, Crustacea

MOFFETT, W. L., AND W. S. FISHER. 1978. Ammonia production rates of *Artemia salina* under various culture conditions. J. Fish. Res. Board Can. 35: 1643–1648.

On utilise *Artemia salina* comme nourriture vivante dans la culture de plusieurs espèces de crustacés et leurs métabolites s'ajoutent à ceux des espèces cultivées. Comme l'ammoniaque est toxique, nous avons suivi sa production durant des périodes de 7 jours pendant que des nauplii et des adultes de *A. salina* étaient maintenus dans diverses conditions de culture. La production d'ammoniaque augmente avec l'élévation de la température entre 15 et 25°C, selon la relation.

$$NH_3 + NH_4^+ \text{ (mg/g poids sec par jour)} = 0.646\ (°C - 10.3)$$

La production d'ammoniaque par les nauplii dépend de la densité. Chez les adultes, il n'y a pas de changement dans la production d'ammoniaque avec un changement dans

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la densité (200–2 000 *A. salina*/L), la salinité (10–50‰) ou le pH (7.0–9.0), ou quand les artémies sont nourries deux fois par jour à 50 000–100 000 cellules de *Platymonas* sp./mL). *Artemia salina* offert ad lib. en nourriture à des homards d'élevage expérimental contribuerait environ 46% de l'ammoniaque totale dans le système de culture.

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Most aquatic animals are ammonotelic, converting the end products of nitrogenous catabolism predominantly to ammonia (Campbell 1973). The ammonia is toxic and must be passed to the environment through gills or excretory openings. Aquatic organisms in nature normally live in quantities of water able to dilute the excreted ammonia. However, in aquaculture rearing systems that maintain high animal densities, removal of this toxic substance becomes an economically important consideration due to discharge limitations and potential water reuse (Botsford et al. 1977).

The ammonia produced by live foods in aquaculture rearing systems adds to that produced by the cultured species. Brine shrimp, *Artemia salina* (Leach), are used successfully as a live food for a variety of aquaculture species, especially crustaceans (Rice and Williamson 1970). For this reason, it is important to determine rates of ammonia production by *A. salina* under various culture conditions. In this study, ammonia production was measured while *A. salina* were held in selected environmental conditions that varied temperature, feeding, animal density, salinity, and pH.

Materials and methods — Experiments were run in 12.5-cm diam × 18.5-cm high glass jars with transparent lids. They were filled with 1.5 L of filtered (1 μm), sterilized (ultraviolet irradiation) seawater containing <1 μg/L $NH_3 + NH_4^+$. Water was heated with aquarium heaters or cooled in a water bath. Airstone aeration was regulated to each jar at approximately 250 mL/min for 4 of every 15 min throughout the experiments.

Temperature and water quality of each jar were monitored daily. Except for the experiments testing these variables, dissolved oxygen was maintained at 5.0–7.5 mg/L, pH at 8.0 ± 0.2, and salinity at 34 ± 1‰. Initial ammonia levels were determined from 15-mL samples employing a Technicon Auto Analyzer which utilizes a colorimetric method to measure total ammonia ($NH_3 + NH_4^+$). Calibration was linear at 5–25 μg-atoms N/L (= .07–28 mg $NH_3 + NH_4^+$/L) and samples with higher concentrations were diluted to within this range. All experimental and sampling apparatus was acid washed and rinsed 3 times in distilled water before use.

Adults of *A. salina* were obtained twice weekly from San Francisco Bay Brand between April and June 1976 and held for 1–2 d in a 100-L seawater tank at 18°C with continuous aeration and were not fed before experimentation. Due to the methods of collection, all *A. salina* used in Experiments 1–6 were sexually mature adults (50–80% were females). Wet weights for adult *A. salina* were determined by collecting them in a net and allowing time to drain 10 min before weighing and counting. The average wet weight over 10 trials was 7.7 mg/adult *A. salina*. Dry weights have been determined to be 10% of the wet weight (Gallagher and Brown 1975).

Nauplii of *A. salina* were obtained as cysts from Metaframe and were hatched at 28°C and 34 ± 1‰ salinity 24 h before the start of the experiments. Nauplii densities were estimated by aliquot and serial dilution. Nauplii wet weights were determined by wetting, suctioning, and weighing filter paper with and without *A. salina* nauplii. This was repeated 10 times, giving an average nauplius wet weight of 14 ± 2 μg. This is consistent with the nauplius wet weight obtained by Gibor (1957) who established the dry weight of 14-μg nauplii to be 2 μg.

All animals were held unfed except those in Experiment 4, which were fed the alga *Platymonas* sp. (U.S. catalog No. 818) in the following manner: *A. salina* were held within a plastic frame basket (0.84-mm mesh Nytex screen) placed inside the glass jars. For 1 h twice daily the baskets and *A. salina* were placed in seawater with algal cell concentrations of 50 000–100 000 cells/mL to insure maximum ingestion rates (Reeve 1963a). They were then rinsed in freshly filtered (1 μm), ultraviolet irradiated seawater to remove any adherent algae and were returned to the experimental glass jars. Time outside the experimental vessels (2 h/d) was compensated for in the data analysis. Clearing of the algal suspension was observed during the feeding period; however, a controlled experiment was run separately to determine ingestion rates. Twelve 1-L Erlenmeyer flasks were washed and rinsed 3 times with distilled water. Ten of these flasks were filled with 500 mL of 1-μm filtered, ultraviolet irradiated seawater, *Platymonas* sp. at a concentration of 67 325 cells/mL, and 1.54 g (wet wt) adult *A. salina* (400 *A. salina*/L). One flask held only seawater and algae (67 325 cells/mL) and one flask held only seawater and *A. salina* adults (400/L). Initial and final algal cell counts were made on a Electrozone/Celloscope Particle Counter (Model No. 112TSN). The duration between the original and final cell count was 1–2 h. Ingestion rates were determined by correcting count differences to account for background seawater particles, decrease due to algal adherence on the vessel walls, added particles due to the presence of *A. salina*, and different sample durations.

The salinity was varied (10–50‰) in Experiment 5 by addition of Instant Ocean to seawater for the higher concentrations and by dilution of seawater using distilled water (with negligible ammonia content) for the lower concentrations. The pH (7.0–9.0) in Experiment 6 was maintained by daily addition of KOH or HCl.

The culture water in experiments involving adults (1–6) was sampled before *A. salina* were added and 5–7 times thereafter over a 7-d experimental period; in Experiment 7, involving nauplii, water was sampled daily for 4 d. Duplicates of each water sample were processed in the Technicon Auto Analyzer. Production rates of ammonia by *A. salina* were determined in all experiments by first calculating the daily change in total ammonia concentration, adjusting for the 1.5-L volume, summing the results, and dividing by the

TABLE 1. Culture conditions and results for Experiments 1–7. The last column describes the amount of toxic ammonia produced (NH_3 only), a result derived from the total ammonia production and the culture conditions according to the equation of Whitfield (1974).

Experiment	Density (shrimp/L)	Dry wt (mg/shrimp)	Temp (°C)	Salinity (‰)	pH	$NH_3 + NH_4^+$ (mg/g per day)	NH_3 (mg/g per day)
1	200	.77	15	34	8.0	2.92	.063
	400					3.37	.073
	800					3.55	.076
	1600					3.15	.069
2	200	.77	20	34	8.0	4.94	.153
	400					5.75	.179
	800					5.91	.184
	1600					6.38	.199
3	200	.77	25	34	8.0	11.49	.513
	400					8.89	.398
	800					8.94	.399
	2000					9.47	.422
4 (fed)	200	.77	25	34	8.0	13.97	.623
	400					10.03	.447
	800					8.79	.392
	1600					9.54	.426
5	400	.77	25	10	8.0	8.37	.438
	400			15		8.81	.447
	400			20		7.83	.386
	400			34		7.79	.348
	400			50		7.73	.306
6	400	.77	25	34	7.0	8.12	.037
	400				7.5	8.57	.124
	400				8.0	7.67	.342
	400				8.5	6.36	.819
	400				9.0	6.59	2.10
7 (nauplii)	1000	.002	13	34	8.0	5.50	.103
	3000					4.66	.087
	6000					3.66	.068
	9000					3.66	.068

number of days in the experiment. Accounting for the dry weight of the *A. salina* results in the recorded units, milligrams ($NH_3 + NH_4^+$) per gram (dry weight) per day.

The data were subjected to fixed analysis of variance (Model I). Lines of regression with $r > .9$ were used in some cases to estimate missing replicates. Tukey's Multiple Range Test was used as an apostori test of differences among means where significant f ratios were observed. Levels of un-ionized ammonia were obtained by incorporating the amount of total ammonia and the various environmental conditions into the following equation from Whitfield (1974):

$$(1)\quad NH_3 = (NH_3 + NH_4^+)/1 + 10^{(pka - pH) + 0.0324\,(25 - °C)}$$

where $pka = 9.2215 + 0.1555\,I + 0.235\,e^{-7I}$ (derived by T. Gossard of the Bodega Marine Laboratory to fit data from Whitfield 1974) and the ionic strength

$$I = 19.9273\,(S‰)/1000 - 1.005109\,(S‰)$$

Results — The experimental design and results are presented in Tables 1 and 2. No significant differences (.05 level) in daily ammonia production were caused by altering the density of adults from 200–2000 animals/L. There was significantly more ($P < .05$) ammonia produced by the lowest density of nauplii in Experiment 7.

The lack of significant differences among ammonia

TABLE 2. Statistical analysis of the data; only the F ratios for temperature and naupliar densities are significant.

Effect of density (Experiments 1–3)	$F_{3,72} = 0.04$
Effect of temperature (Experiments 1–3)	$F_{2,72} = 14.3$
Effect of feeding vs. starvation (Experiments 3–4)	$F_{1,48} = 0.4$
Effect of salinity (Experiment 5)	$F_{4,30} = 0.05$
Effect of pH (Experiment 6)	$F_{4,35} = 0.04$
Effect of density on nauplii (Experiment 7)	$F_{3,24} = 7.2$

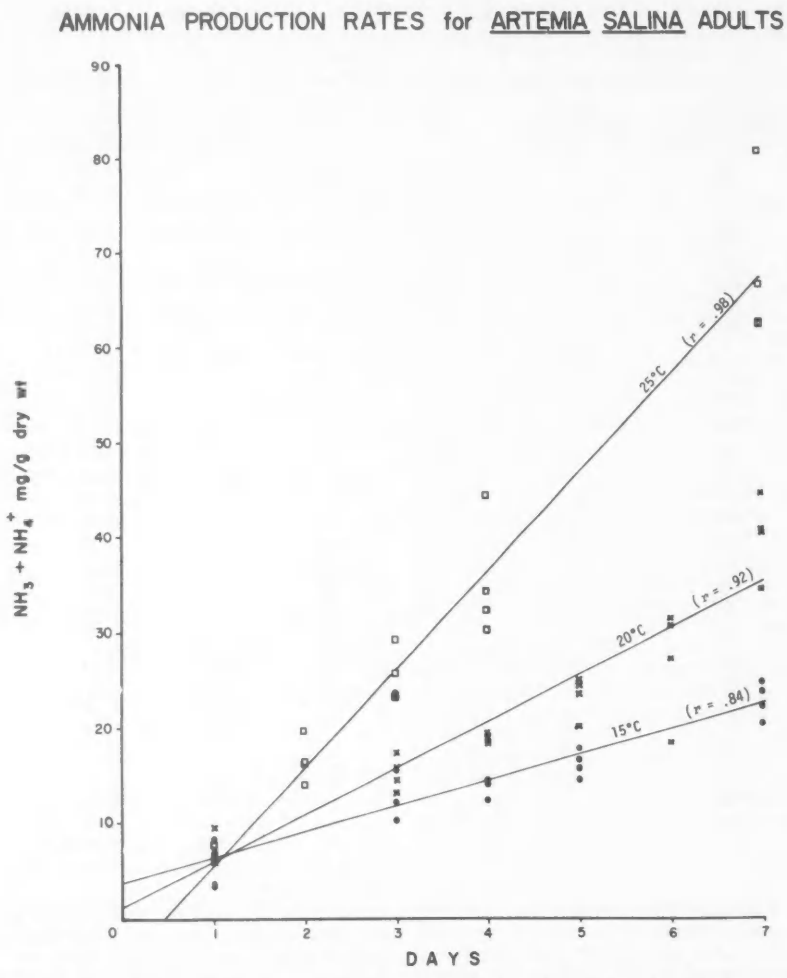

FIG. 1. Temperature effects on total ammonia production of *Artemia salina* adults using all densities tested. The mean rates of production are 3.24, 5.74, and 9.70 mg/g per day for 15, 20, and 25°C.

production rates by adults at different densities allowed the mean of the results of all densities from Experiment 1 (15°C) to be compared with the mean from all densities of Experiments 2 (20°C) and 3 (25°C): these are 3.24, 5.74, and 9.70 mg $(NH_3 + NH_4^+) \cdot g(dry)^{-1} \cdot d^{-1}$ for 15, 20, and 25°C, respectively ($P < .05$). This pronounced increase in total ammonia production with increased temperature (Fig. 1, Table 2) was linear by statistical analysis and described a daily ammonia production rate (within the 15–25°C temperature range) according to the equation

$$(2)\quad NH_3 + NH_4^+ \text{ (mg/g dry wt)} = 0.646\ (°C - 10.3).$$

Q_{10} values calculated from these averages are 3.1 (15–20°C) and 2.9 (20–25°C).

Salinity and pH over the ranges tested caused no significant differences in ammonia production. Feeding with *Platymonas* sp. also caused no significant changes. Adults of *A. salina* fed *Platymonas* sp. in the 10 flasks of a separate experiment ingested an average 16 104 cells/mL per hour (SD ± 1415). The mean ingestion rate was 40 260 cells/*A. salina* per hour. Although analytical comparison of nauplii and adults is not possible due to the density dependence exhibited by the nauplii, Table 1 shows the daily ammonia production per dry weight or nauplii at 13°C (Experiment 7) to be about 1.3 times greater than that of adults held at 15°C (Experiment 1).

Discussion — The most critical effect on ammonia

production by *A. salina* was caused by variations in temperature. Q_{10} values for adult *A. salina* ammonia production are similar to Q_{10} values for oxygen consumption of other Crustacea (Wolvekamp and Waterman 1960) and are comparable to the effect of temperature on acceleration of chemical reactions (Prosser 1973). This last observation suggests that the increasing temperature effects are the result of enhanced chemical or enzymatic reactions unrestricted by any limiting factors (such as the lack of food).

A second influential factor involved in ammonia production by *A. salina* was the size or age of the animal. Comparison of Experiment 1 (adults at 15°C) with Experiment 7 (nauplii at 13°C) showed that nauplii produced approximately 1.3 times the ammonia as the adults on a dry weight basis, and nearly twice that by wet weight. This is consistent with the findings of Gilchrist (1958) who showed that the O_2 consumption of *A. salina* decreased with increased body weight (dry). Zeuthen (1947), using O_2 consumption/total body nitrogen, found this pattern repeated in several Crustacea. Since ammonia and oxygen are exchanged equally in amino acid catabolism, it is reasonable to assume that ammonia production rates are similar to metabolism which is determined by oxygen consumption rates.

There were no significant differences between the ammonia production rates of fed and unfed *A. salina* (Table 2). Adult *A. salina* were able to ingest *Platymonas* sp. at a rate (40 260 cells/*A. salina* per hour) similar to that which Reeve (1963b) found to be optimal. Radioactive (^{14}C) labeling has shown incorporation of algal cell material into *A. salina* tissue (Cohen et al. 1976), although no studies of nitrogen or protein assimilation are available. Conversion efficiencies vary widely: Harvey (1950) showed that some zooplankton were 70% efficient, Gibor (1957) found *A. salina* to be 53% efficient, and Reeve (1963a) observed variations from 26 to 76% efficiency for *A. salina* depending on the cell concentration offered the animals. From these studies we conclude that the fed *A. salina* of Experiment 4 were at least partially converting the algae to animal tissue. Since the animals of Experiment 3 were unfed, their metabolism must be considered "non-tissue-forming" (Reeve 1963a), and the ammonia produced must have been catabolized from stored reserves. This is supported by the evidence (Chaplin 1967, cited in Florkin and Scheer 1971) of a decrease in free amino acid pools in starved *A. salina*.

Experiments involving adults indicated no significant differences in the ammonia production rate due to stocking density (Table 2). The nauplii held at 13°C, however, showed a significantly elevated ammonia production rate at the lowest density. This may reflect increased activity due to increased space or high density related stress that inhibits metabolism. This trend is also indicated for adults at 25°C (Experiments 3 and 4) (Table 1); the lack of significant increase at the .05 level is possibly due to an insufficient range in experimental densities.

Generally, crustaceans are expected to consume more oxygen and excrete more ammonia in hypotonic than in hypertonic environments (Campbell 1973). In hypotonic conditions, activity of 3-glycerophosphate dehydrogenase increases to catabolize amino acids, causing a decrease in free amino acids and an increase in both oxygen consumption and ammonia excretion (Emerson 1969). Conversely, in the hypertonic environment ammonia is used by the animal for glutamate synthesis (activation of glutamate dehydrogenase) which is transaminated to produce other amino acids (free amino acids increase in hypertonic environments).

There is some controversy, however, whether *A. salina* follow this general trend. Decreasing respiration with increased salinity has been reported for *A. salina* cysts (Emerson 1967), nauplii (Engel and Angelovic 1968), and for the entire *A. salina* life cycle (Eliassen 1952). However, Gilchrist (1956), using adult females, and Kratowich (1964), using nauplii, found no salinity effects on respiration. The results of this study (Experiment 5) using *A. salina* adults at 10–50‰ salinity showed no significant change in ammonia production, although a decrease can be noted at salinities >15‰. The hemolymph of *A. salina* is isotonic at about 10‰ (Robertson 1960); therefore, osmotic regulation was required at the other salinities tested.

Environmental pH (Experiment 6) had no effect on the ammonia production rate (Table 2). However, environmental pH has a dramatic effect on the excreted ammonia (Table 1). The un-ionized (NH_3) form increased over 50 times as pH increased from 7.0 to 9.0 while the total ammonia ($NH_3 + NH_4^+$) remained unchanged. This is particularly important to aquaculturists due to the toxicity of un-ionized NH_3.

In aquaculture, ammonia produced by *A. salina* can be a significant addition to that produced by the cultured species. For example, about 1000, 2-g wet wt juvenile American lobsters (*Homarus americanus*) are held in a typical experimental rearing system at 21°C. Ad lib. feeding should be about 5% of the lobster wet weight per day (Shleser and Gallagher 1974) or, in this case, 100 g dry wt *A. salina*. With constant feeding by the lobsters (Conklin et al. 1978) the live *A. salina* population for a full day would be equivalent to ½ the initial population, or 50 g dry wt. Applying the ammonia production rate equation (2), 50 g *A. salina* adults at 21°C add 345.6 mg $NH_3+NH_4^+$/d to the lobster culture system. Two-gram lobsters produce nearly 0.2 mg $NH_3+NH_4^+$/g wet wt each day (unpublished results), or 400 mg/d for the 1000 lobsters in the system. Therefore, with ad lib feeding, the live food *A. salina* will contribute roughly 46% of the ammonia in the culture system. Due to the toxicity of ammonia to marine animals, the ammonia must be removed by water exchange or biological filtration.

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COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

Modification of the rheotropic behavior of male rainbow trout (*Salmo gairdneri*) by ovarian fluid **M. E. Emanuel and J. J. Dodson**

Deepwater exchange processes in the Saguenay Fjord **G. H. Seibert, R. W. Trites, and S. J. Reid**

Periodicities in Atlantic Coast striped bass (*Morone saxatilis*) commercial fisheries data **W. Van Winkle, B. L. Kirk, and B. W. Rust**

Paralytic shellfish toxins in the sea scallop, *Placopecten magellanicus*, in the Bay of Fundy **C. P. Hsu, A. Marchand, Y. Shimizu, and G. G. Sims**

Entrainment of larval fish by the Douglas Point generating station, Lake Huron, in relation to seasonal succession and distribution **J. R. M. Kelso and J. K. Leslie**

Characterization of particulate organic matter transported by some Cascade Mountain streams **R. J. Naiman and J. R. Sedell**

An automated device (AGARS) for studying avoidance of pollutant gradients by aquatic organisms **C. R. Cripe**

Phytoplankton ecology of Vancouver Harbor **J. G. Stockner and D. D. Cliff**

Meristic variation of *Lycodapus mandibularis* (Pisces: Zoarcidae) and oceanic upwelling on the west coast of North America **A. E. Peden**

Notes

Prococious sexual development in hatchery-reared and laboratory-maintained male steelhead trout (*Salmo gairdneri*) **S. P. Schmidt and E. W. House**

Survival and growth of juvenile American lobsters (*Homarus americanus*) after eyestalk ablation **D. J. Trider, E. G. Mason, and J. D. Castell**

Comparison of a high volume pump and conventional plankton nets for collecting fish larvae entrained in power plant cooling systems **R. M. Leithiser, K. F. Ehrlich, and A. B. Thum**

Influences of dieldrin on the growth and body composition of fingerling rainbow trout (*Salmo gairdneri*) fed Oregon Moist Pellets or tubificid worms **G. Phillips and D. R. Buhler**

Sublethal effects of environmental acidification on rainbow trout (*Salmo gairdneri*) **C. M. Neville**

Myxosoma cerebralis: a method for staining spores and other stages with silver nitrate **K. Wolf and M. E. Markiw**

Perspectives

Maybe you can't get there from here: a foreshortened history of research in relation to management of Pacific salmon **P. A. Larkin**

RECENT PUBLICATIONS/RECENTES PUBLICATIONS

The number following each title in each series refers to the establishments listed at the end of the section. Inquiries concerning any particular item should be directed to the issuing establishment.

Les nombres qui suivent les titres de chacune des séries désignent les établissements suivants à la fin de la section. Pour toute demande de renseignements concernant un rapport particulier, il faut s'adresser au service responsable.

Technical Report Series

Technical Reports are research documents that are of sufficient importance to be preserved, but which for some reason are not appropriate for primary scientific publication. Inquiries concerning any particular Report should be directed to the issuing establishment.

733. ANDERSON, T. C., AND B. P. MCDONALD. 1978. A portable fence for counting fishes in rivers. Fish. Mar. Serv. Tech. Rep. 733: 13 p. (9)

734. RAY, S., AND J. COFFIN. 1977. Ecological effects of cadium pollution in the aquatic environment: A Review. Fish. Mar. Serv. Tech. Rep. 734: 24 p. (8)

735. LAVOIE, R. E. 1977. The oyster population of the public fishing area, Caraquet Bay, New Brunswick. Fish. Mar. Serv. Tech. Rep. 735: 39 p. (8)

736. SMITH, J. 1977. Catch and effort statistics of the Canadian groundfish fishery on the Pacific coast in 1976. Fish. Mar. Serv. Tech. Rep. 736: 83 p. (1)

737. ZITKO, V. 1971. Uptake and excretion of chlorinated and brominated hydrocarbons by fish. Fish. Mar. Serv. Tech. Rep. 737: 14 p. (6)

738. SIBERT, J., B. A. KASK, AND T. J. BROWN. 1977. A diver-operated sled for sampling the epibenthos. Fish. Mar. Serv. Tech. Rep. 738: 19 p. (1)

739. TSUYUKI, H., J. CHENG, S. N. WILLISCROFT, AND M. D. HUYNH. 1977. Causes of development of sponginess in roe produced from frozen herring. Fish. Mar. Serv. Tech. Rep. 739: 21 p. (2)

740. STOCKNER, J. G. 1977. Lake fertilization as a means of enhancing sockeye salmon populations: The state of the art in the Pacific northwest. Fish. Mar. Serv. Tech. Rep. 740: 14 p. (1)

741. FEE, E. J. 1977. A computer program for estimating annual primary production in vertically stratified waterbodies with an incubator technique. Fish. Mar. Serv. Tech. Rep. 741: 38 p. (4)

742. SAMEOTO, D. D. 1977. Zooplankton biomass, density and their association with phytoplankton on the southwest area of the Nova Scotia shelf. Fish. Mar. Serv. Tech. Rep. 742: 30 p. (7)

743. ALDERDICE, D. F., R. A. BAMS, AND F. P. J. VELSEN. 1977. Factors affecting deposition, development, and survival of slamonid eggs and alevins. A bibliography, 1965–1975. Fish. Mar. Serv. Tech. Rep. 743: 276 p. (1)

744. ACARA, A. H. 1977. The Meadow creek spawning channel. Fish. Mar. Serv. Tech. Rep. 744: 91 p. (1)

745. WELCH, H. E., P. E. K. SYMONS, AND D. W. NARVER. 1977. Some effects of potato farming and forest clear-cutting on small New Brunswick streams. Fish. Mar. Serv. Tech. Rep. 745: 13 p. (6)

Rapports techniques

Les rapports techniques sont des documents de recherche qui revêtent une assez grande importance pour être conservés mais qui, pour une raison ou pour une autre, ne conviennent pas à une publication scientifique de fonds. Pour toute demande de renseignements concernant un rapport particulier, il faut s'adresser au service responsable.

746. PHILLIPS, A. C. 1977. Key field characters of use in identifying young marine Pacific salmon. Fish. Mar. Serv. Tech. Rep. 746: 13 p. (1)

747. KOHLER, A. C., D. J. FABER, AND N. J. MCFARLANE. 1977. Eggs, larvae and juveniles of fishes from plankton collections in the Gulf of St. Lawrence during 1972 to 1975. Fish. Mar. Serv. Tech. Rep. 747: 180 p. (6)

748. CLARKE CRAIG, W., W. GRIFFIOEN, AND A. SOLMIE. 1977. A factorial mating study comparing the fertility of pen-reared and wild coho salmon (*Oncorhynchus kisutch*). Fish. Mar. Serv. Tech. Rep. 748: 9 p. (1)

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751. WHYTE, J. N. C., AND J. R. ENGLAR. 1977. Aspects of the production of herring roe in *Macrocystis Integrifolia* in Georgia strait locations. Fish. Mar. Serv. Tech. Rep. 751: 28 p. (2)

752. FRASER, F. J., D. D. BAILEY, AND M. J. WOOD. 1978. Big Qualicum river salmon development project (Vol. III). Experimental rearing of chum salmon juveniles (*Oncorhynchus keta*) in fresh water (1968–1970). Fish. Mar. Serv. Tech. Rep. 752. (12)

753. KRAMER, D. E., D. M. A. NORDIN, AND L. J. GARDNER. 1977. A comparison of the quality changes of Alaska pollock and Pacific cod during frozen storage at −28°C. Fish. Mar. Serv. Tech. Rep. 753: 63 p. (2)

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758. STOCKNER, J. G., AND A. C. COSTELLA. 1978. Benthic algae in the Thompson river, British Columbia: Their response to pulpmill and sewage effluent. Fish. Mar. Serv. Tech. Rep. 758: 19 p. (1)
759. SHEPHERD, B. G., AND R. M. J. GINETZ [ed.] 1978. Proceedings of the 1977 Northwest Pacific chinook and coho salmon workshop. Fish. Mar. Serv. Tech. Rep. 759: 164 p. (3)

Data Reports

These reports provide a medium for filing and archiving data compilations where little or no analysis is included. Such compilations commonly will have been prepared in support of other journal publications or reports. The subject matter of Data Reports reflects the broad interests and policies of the Fisheries and Marine Service, namely, fisheries management, technology and development, ocean sciences and aquatic environments relevant to Canada.

Numbers 1–25 in this series (except No. 24 issued by Newfoundland Region, St. John's, Nfld.) were issued as Fisheries and Marine Service Data Records by the Pacific Biological Station, Nanaimo, B.C. The series name was changed with report number 26.

Rapports statistiques

Ces rapports servent de base à la compilation des données de classement et d'archives pour lesquelles il y a peu ou point d'analyse. Cette compilation aura d'ordinaire été preparée pour appuyer d'autres publications ou rapports. Les sujets des Rapports statistiques reflètent la vaste gamme des intérêts et politiques du Service des pêches et de la mer, notamment gestion des pêches, techniques et développement, sciences océaniques et environnements aquatiques, au Canada.

Les numéros de 1 à 25 de cette serie (sauf le nº 24, publié par région de Terre-Neuve, St-Jean, T.-N.) ont été publies à titre de Records statistiques, Service des pêches et de la mer, par la Station biologique de Pacifique, Nanaïmo, (C.-B.). Le nom de la série a été modifie à partir du numéro 26.

43. QUAY, P., R. H. HESSLEIN, W. S. BROECKER, AND D. W. SCHINDLER. 1978. Measurement of vertical and horizontal diffusion rates in Experimental lakes and water column enclosures using injections of tritiated water. Fish. Mar. Serv. Data Rep. 43: 39 p. (4)
44. BARNER, L. W., AND F. H. C. TAYLOR. 1977. Herring survey off southwest Vancouver island. Fish. Mar. Serv. Data Rep. 44: 17 p. (1)
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46. PERCY, J. A., AND J. WALBRIDGE. 1977. Seasonal changes in organic composition and caloric value of an arctic marine amphipod *Onisimus* (*-Boeckosimus*) *affinis*. Fish. Mar. Serv. Data Rep. 46: 28 p. (5)
47. RICHARD, D. M. 1977. Surveys of thirteen lakes in Antigonish and Guysborough counties, Nova Scotia, 1976. Fish. Mar. Serv. Data Rep. 47: 37 p. (8)
48. BEAMISH, R. J., M. SMITH, AND R. SCARSBROOK. 1978. Hake and pollock study, Strait of Georgia cruise, *G. B. Reed* — January 6–February 21, 1975. Fish. Mar. Serv. Data Rep. 48: 206 p. (1)
49. FULTON, J. 1978. Seasonal and annual variations of net zooplankton at ocean station P, 1965–1976. Fish. Mar. Serv. Data Rep. 49: 89 p. (1)
50. CASS, A. J., R. J. BEAMISH, M. S. SMITH, AND J. R. SCARSBROOK. 1978. Hake and pollock study, Strait of Georgia cruise *G. B. Reed* — March 17–24, 1975. Fish. Mar. Serv. Data Rep. 50: 66 p. (1)
51. DAVENPORT, D., AND R. M. WALLIS. 1978. *Arctic Harvester* groundfish cruise no. 77-3 (October 11–28, 1977). Fish. Mar. Serv. Data Rep. 51: 16 p. (1)
52. MARSHALL, D. E., R. F. BROWN, V. D. CHALLEY, AND D. G. DEMONTIER. 1978. Preliminary catalogue of salmon streams and spawning escapements of satistical area 2W (Queen Charlotte Islands). Fish. Mar. Serv. Data Rep. 52: 258 p. (2)
53. MOSHENKO, R. W., AND G. LOW. 1978. Lake whitefish, *Coregonus clupeaformis* (Mitchill), from the commercial fishery of Great Slake Lake, Northwest Territories, 1975–76. Fish. Mar. Serv. Data Rep. 53: 16 p. (4)

Translation Series

The following translations have been prepared by or for the Fisheries and Marine Service, for use in its investigations. Copies are available from Translation Services, Canada Institute for Scientific and Technical Information, National Research Council of Canada, Ottawa, Ontario K1A 0S2, at a cost of 22¢ per page and a minimum charge of $2.20. Information on translations can be obtained from the Scientific Information and Publications Branch.

Traductions

Les traductions dont il est question ci-après ont été préparées par ou pour le Service des pêches et des sciences de la mer, à des fins de recherche. On peut en obtenir des exemplaires, à 22¢ la page et à un prix minimum de $2.20 aux Services de traduction, Institut canadien de l'information scientifique et technologique, Conseil national de recherches du Canada, Ottawa (Ontario), K1A 0S2. La Direction de l'information et des publications scientifiques peut fournir des renseignements sur ces traductions.

INUKAI, K. 1976. Rate of spoilage of frozen mackerel after thawing. Mie Igaku 20: 19–24. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 4379, 1978)

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KAMENTSEV, V. 1972. Instructions for the measurement of mesh sizes in fishing gear used in the north Atlantic. Ministerstvo Rybnogo Khozyaistva SSSR. Prikaz No. 337, October 10, 1972. 15 p. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 4382, 1978)

TANAKA, K. 1970. Freezing preservation of fresh sea urchins (gonad). Reito 45: 925–931. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 4383. 1978)

IIOKA, C., ET AL. 1977. An examination of the release of seawater-reared fingerlings. Iwate Ken Suisan Shikenjo Hokoku-sho, March, 33 p. (Report from the Fisheries Research Station of Iwater Prefecture.) (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 4384)

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ANON. [Undated]. Fishing gear and technology. Cuban Fishing Fleet, Technical Section, 132 p. (Transl. from Spanish by Fish. Mar. Serv. Transl. Ser. No. 4389, 1978)

TAKAGAKI, T. 1978. Lipids (II). Yukagaku 27: 172–176. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 4390, 1978)

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ANNOUNCEMENTS/AVIS

Culture of Exotic Fishes

Proceedings of a Symposium

This report, published by the Fish Culture Section of the American Fisheries Society, consists of 22 papers (250 printed pages) that were presented at the symposium held at Aquaculture/Atlanta/'78. It deals primarily with tilapia and Chinese carp species under various production systems: monoculture, polyculture, hybrids, sex reversed, increased production with organic fertilization, biological weed control, test marketing study.

To order a copy please send a cheque or money order (US $5 for mailings in USA and Canada, US $6 for mailings to other countries) to Dr D. D. Moss, Fisheries Department, Auburn University, Auburn, Ala. 36830, USA.

Culture des poissons exotiques

Comptes rendus d'un symposium

Ce rapport, publié par la section pisciculture de l'American Fisheries Society, comprend 22 articles (250 pages imprimées) présentés au symposium tenue à Aquaculture/Atlanta/'78. Il porte surtout sur *Tilapia* et les espèces de carpes chinoises dans divers systèmes de production : monoculture, polyculture, hybrides, inversion des sexes, augmentation de la production avec engrais organiques, contrôle biologique des herbes, études de marketing expérimental.

On pourra se procurer un exemplaire en adressant un chèque ou mandat-poste ($5 E.-U. pour expédition aux Etats-Unis et au Canada, et $6 E.-U. pour expédition aux autres pays) au Dr D. D. Moss, Fisheries Department, Auburn University, Auburn, Ala. 36830, USA.

Canadian Conference For Fisheries Research
Canadian Society of Environmental Biologists

The thirty-second Annual Meeting of the CCFFR will be held at the Holiday Inn, 107th Street and 100th Avenue, Edmonton, Alberta, T5I 1J1, January 3 and 4, 1979. Fisheries and Marine Service, Department of Fisheries and the Environment, will sponsor this meeting. The President is J. C. Stevenson and the Secretary-Treasurer is J. Camp, both of Fisheries and Marine Service, Department of Fisheries and the Environment, Ottawa. Program Chairman is L. Johnson, Freshwater Institute, Fisheries and Marine Service, Department of Fisheries and the Environment, Winnipeg.

The Canadian Society of Environmental Biologists will also meet at the Holiday Inn, Edmonton, January 4 and 5, 1979. The President is B. Lister, Envirocon Ltd., West Vancouver. The Secretary-Treasurer is R. M. Biette, Ontario Ministry of Natural Resources, Toronto, and the Program Chairman is D. J. Neave, Fish and Wildlife Division, Edmonton. Local arrangements for CCFFR and CSEB were under the Chairmanship of J. S. Nelson, University of Alberta, Edmonton.

Members are encouraged to make their hotel reservations as soon as possible. Confirmed arrangements are: Single room, $30; Twin room, $36; Student 4/room at $9 each. $36; Holiday Inn — (403) 429-2861.

Note: The airport bus into downtown Edmonton is the least expensive transportation. The bus normally does not stop at the Holiday Inn. However, it comes within a few blocks and may stop if there are several requests.

CCFFR Preliminary Program

Tuesday, January 2, 1900–2100 h — Advance Registration

Wednesday, January 3, 0900–1200 h — Migrations Within a Homogeneous Medium. (*Convener:* K. Chang-Kue, Department of Fisheries and the Environment, Freshwater Institute, Winnipeg, Manitoba (204) 265-7379.) Inconnu in Alaska by K. T. Alt; Capelin in Newfoundland by J. Carscadden; Shad in eastern North America by W. Leggett; A paper on whales, speaker to be announced later.

Wednesday, January 3, 1400–1700 h — Contributed Papers. (*Convener:* R. Hartland-Rowe, University of Calgary, Calgary, Alberta (403) 284-5261.) Members interested in presenting a paper should immediately contact the Convener.

Wednesday, January 3, 2000 h — Smoker in Flanagan's Room (no host drinks at $1.35). (P. A. Larkin, Guest Speaker)

Thursday, January 4, All day joint CCFFR–CSEB Session — Problems and Opportunities in the Peace–Athabasca River System. (*Convener:* S. B. Smith, Alberta Oil Sands Environmental Research Program, (403) 427-3096.)

Thursday, January 4, approx. 1630 h — CCFFR Business Meeting.

CSEB Preliminary Program

Thursday, January 4, approx. 1800 h — CSEB Annual Banquet and Business Meeting.

Friday, January 5, 0900 h — Review of Wildlife Legislation and Legal Problems in Canada: A four-member panel chaired by G. Campbell (403) 427-6749 will provide background expertise and discussion on the evolution of wildlife law, special statutes, constitutional responsibilities and constraints together with consideration of the adequacy or inadequacy of current legislation to protect wildlife resources; *Biologists Role in Public Communications:* A session chaired by D. McDonald (403) 427-6749 will discuss the need and opportunities for biologists to become more involved in public communications in order to protect wildlife resources; *Contributed Papers:* (*Chairman:* L. Carbyn, Canadian Wildlife Service, 10025 Jasper Avenue, Edmonton, Alberta (403) 425-6860.) This session may be combined with CCFFR if very few papers are received.

Note: This is a call for papers for the three topics mentioned above. Those interested in presenting a paper should contact the session Chairman directly.

Saturday, January 6 — Field trip to Fort McMurray and tarsands, arranged by Neil Chymko.

We also have been advised that the Society of International Limnologists (SIL) will be holding an Annual Meeting on January 6 at the Holiday Inn, after the CSEB/CCFFR Meeting concludes. Major emphasis will be on the effects of acidification on fish and habitats.

Publications diverses spéciales

Office des recherches sur les pêcheries du Canada à 1898 à 1973
J. C. STEVENSON
(1973, 18 p., nº de cat. Fs 41-31/20; gratuit) [*bilingue*]
S'adresser au Ministère des Pêches et Océans, Direction de l'information et des publications scientifiques, 240, rue Sparks, 7e étage ouest, Ottawa, Canada K1A 0E6

L'Homme, les lacs et la prolifération des algues
J. R. VALLENTYNE
(1978, 196 p., nº de cat. Fs 41-31/22F; Canada $3.75, autres pays $4.50)
S'adresser à : Approvisionnements et Services Canada, Imprimerie et édition, Ottawa, Canada K1A 0S9

Méthodes de détection de certains agents pathogènes chez les salmonidés
D. C. GILLESPIE, T. P. T. EVELYN, C. FRANTSI, R. M. MACKELVIE ET N. NEUFELD
(1974, 21 p., nº de cat. Fs 41-31/23; gratuit) [*bilingue*]
S'adresser au Ministère des Pêches et Océans, Direction des recherches sur les pêches, 240, rue Sparks, Ottawa, Canada K1A 0S9

Poissons de la région de la capitale du Canada
DON E. MCALLISTER ET BRIAN W. COAD
(1974, 200 p., nº de cat. NM 92-43/1974; Canada $4.00, autres pays $4.80) [*bilingue*]
S'adresser aux Musées Nationaux du Canada, Direction des publications et du marketing, 491, rue Bank, Ottawa, Canada K2P 1Z2

Guide pratique de l'anatomie et de la physiologie du saumon du Pacifique
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Volume 35, No. 12, December 1978 Volume 35, nº 12, décembre 1978

Announcements/Avis 1517

Ichthyoplankton of the St. Lawrence estuary: composition, distribution, and abundance **K. W. Able** 1518–1531

Modification of phosphorus retention models for use with lakes with low areal water loading **M. L. Ostrofsky** 1532–1536

Life history and taxonomic status of an isolated population of Arctic char, *Salvelinus alpinus*, from Gros Morne National Park, Newfoundland **P. J. Rombough, S. E. Barbour, and J. J. Kerekes** 1537–1541

Changes in gill ATPase activity and smolt status of Atlantic salmon (*Salmo salar*) **R. L. Saunders and E. B. Henderson** 1542–1546

The petroleum-inducible mixed-function oxidase of cunner (*Tautogolabrus adspersus* Walbaum 1972): some characteristics relevant to hydrocarbon monitoring **D. G. Walton, W. R. Penrose, and J. M. Green** 1547–1552

The Lake Washington ecosystem: the perspective from the fish community production and forage base **D. M. Eggers, N. W. Bartoo, N. A. Rickard, R. E. Nelson, R. C. Wissmar, R. L. Burgner, and A. H. Devol** 1553–1571

Impact of the introduction of kokanee (*Oncorhynchus nerka*) and opossum shrimp (*Mysis relicta*) on a subalpine lake **M. D. Morgan, S. T. Threlkeld, and C. R. Goldman** 1572–1579

Enhancement of sockeye salmon (*Oncorhynchus nerka*) by lake fertilization in Great Central Lake: summary report **R. J. LeBrasseur, C. D. McAllister, W. E. Barraclough, O. D. Kennedy, J. Manzer, D. Robinson, and K. Stephens** 1580–1596

Daily ration of yellow perch (*Perca flavescens*) from Lake Memphremagog, Quebec–Vermont, with a comparison of methods for in situ determinations **B. S. Nakashima and W. C. Leggett** 1597–1603

Origin of deposited material sedimented in a marine bay **B. T. Hargrave and S. Taguchi** 1604–1613

Loss rates of suspended material sedimented in a marine bay **S. Taguchi and B. T. Hargrave** 1614–1620

Seasonal changes in oxygen uptake by settled particulate matter and sediments in a marine bay **B. T. Hargrave** 1621–1628

Notes

Modified oxidation/fermentation medium for use in identification of bacterial fish pathogens **G. R. Walters and J. A. Plumb** 1629–1630

Numerical model of the circulation in an open bay **B. Petrie and K. Drinkwater** 1631–1635

Separation of two dissolved reactive phosphorus fractions in lakewater **M. T. Downes and H. W. Paerl** 1636–1639

Biological availability of low versus high molecular weight reactive phosphorus **H. W. Paerl and M. T. Downes** 1639–1643

Ammonia production rates of *Artemia salina* under various culture conditions **W. L. Moffett and W. S. Fisher** 1643–1648

Coming next month/À paraître le mois prochain 1649

Recent publications/Récentes publications 1650–1653

Announcements/Avis 1654

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